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CONTENTS OF VOLUME 86 PART 1

Article	Page
1 Movement and Mortality Patterns of Black Ducks and Mountain Ducks Banded in Victoria. By F. I. NORMAN	1
2 Faulting and the Physiography of the Croydon Sunkland, Victoria. By MICHAEL J. GARRETT	15
3 The Biology of Fungi Associated with Root Rot of Subterranean Clover in Victoria. By L. W. BURGESS, H. J. OGLE, J. P. EDGERTON, L. L. STUBBS P. E. NELSON (Plate 1)	19
4 Disjunctions in the Distribution of <i>Eucalyptus</i> Species Between Western Victoria and the Mount Lofty-Flinders Ranges Area, South Australia. By R. F. PARSONS	29
5 Th-230/U-234 Gochronology of Marine Shells from near Sale, E. Victoria, Australa. By JAMES C. SCHORNICK, JR.	35
6 Opisthobranch Molluscs from the Australian Sub-Antarctic Territories of Macquarie and Heard Islands. By ROBERT BURN	39
7 The Distribution of <i>Nothofagus Cunninghamii</i> Rainforest. by TRUDA M. HOWARD and D. H. ASHTON	47
8 Lower Devonian Conodonts from Loyola, Victoria. By B. J. COOPER (Plates 2-3)	77
9 A Computer Simulation Study of Mark-Recapture Methods in Ecology. By G. ETTERS HANK and DAPHNE L. ETTERS HANK	85
<i>Studies on Australian Cainozoic Brachiopods—</i>	
10 (1) The Loop Development of <i>Frenulina sanguinolenta</i> (Gmelin 1790) By JOYCE R. RICHARDSON (Plate 4)	111
11 (2) The Family Laqueidae (Terebratellidae). By JOYCE R. RICHARDSON (Plates 5-6)	117
12 (3) The Subfamily Bouchardiinae (Terebratellidae). By JOYCE R. RICHARDSON (Plate 7)	127
13 Second List of Radiocarbon Dates on Samples from Victoria, Australia. By EDMUND D. GILL	133

CONTENTS OF VOLUME 86 PART 2

Article	Page
14 <i>Nothofagus cunninghamii</i> Ecotonal Stages: Buried Viable Seed in North West Tasmania. By TRUDA M. HOWARD	137
15 Stratigraphic and Isotopic Ages of Tertiary Basalts at Maude and Aireys Inlet, Victoria, Australia. By C. ABELE and R. W. PAGE	143
16 Fossil Penguin Bones from Macquarie Island, Southern Ocean. By A. R. McEVEY and W. J. M. VESTJENS, with Appendix by E. D. GILL (Plates 8-11)	151
17 The Victorian Isograptids and Isograptid-Like Graptoloids. By F. C. BEAVIS and SARA BEAVIS	175
<i>Some papers delivered at the Royal Society Symposium, 'The Urban Environment and Life', September 13, 1973</i>	
18 Design and the Living Environment. By D. G. D. YENCKEN (Plate 12) ..	215
19 Law and Economics. By GEORGE A. KAUFMANN	223
20 Environmental Design of Urban Areas. By BARRY McNEILL	227
Royal Society of Victoria, Officers	
Abridged Report of Council for the Year Ending March 8, 1973	234
Index to Volume 86	235

Papers accepted for publication by the Society and edited under the authority of the Council. The authors of the several papers are individually responsible for the accuracy of the statements made and the soundness of the opinions given therein.

MOVEMENT AND MORTALITY PATTERNS OF BLACK DUCKS AND MOUNTAIN DUCKS BANDED IN VICTORIA

By F. I. NORMAN*

ABSTRACT: Between 1952 and 1969, 5644 Black Ducks and 3798 Mountain Ducks were banded in Victoria. Of these 1461 (25.9 per cent) Black Ducks and 749 (19.7 per cent) Mountain Ducks were recovered to the end of 1969; of those banded 20.8 and 17.2 per cent were shot. By combination of data for all years it is shown that most recoveries were within a year of banding and that the corresponding mortality rate was highest (67.3 per cent for Black Ducks and 48.8 per cent for Mountain Ducks) in the first year after banding. Within four years 93.3 per cent mortality occurred in Black Ducks and 90.4 per cent in Mountain Ducks, with calculated life expectancies being 1.26 and 1.44 years respectively. Life expectancy was greater in males than females, and this held for juveniles which have a higher mortality rate in the year following banding than other groups. However, juveniles and females contained less shotgun pellets than males when fluoroscopically examined; of Black Ducks examined 13.8 per cent carried shot as did 22.3 per cent of the Mountain Ducks.

Calculations based on the average mortality rates indicate that Black Ducks must produce four, and Mountain Ducks two, young per pair annually, to maintain their average population sizes and to sustain the present mean hunting pressure. Though few data are available this would appear feasible for both species, which disperse widely within this state. Habitat preservation will become more important and since there is a movement into and out of the State, conservation will depend in part on co-operative measures.

INTRODUCTION

Amongst the major game species of waterfowl in Victoria, Black Duck *Anas superciliosa* Gmelin, Grey Teal *A. gibberifrons* Müller and Chestnut Teal *A. castanea* (Eyton) form a large portion of the annual harvest of ducks taken during open (shooting) seasons. And although not generally considered important as a game species, the Mountain Duck *Tadorna tadornoides* (Jardine and Selby) is shot both widely and in large numbers. Black Ducks and Mountain Ducks differ in their preferred habitat requirements, though both are extensively distributed. Whereas Black Ducks generally inhabit deeper, more permanent and well-vegetated wetlands, Mountain Ducks are usually seen on or near open wetland areas in coastal regions and inland plains (Frith 1967, Wheeler 1967). Black Ducks have a predominantly vegetarian diet (Frith 1959, 1967, Frith, Braithwaite & McKean 1969) but apparently Mountain Ducks are more omnivorous, eating invertebrates, small vertebrates and plant material (Frith 1967). Mountain Ducks are particularly

numerous in Western Victoria where large flocks cause occasional localized damage to growing crops and pastures.

Little is known about the movement or mortality patterns of Black Ducks or Mountain Ducks in Victoria. Banding provides a convenient method of determining such aspects of waterfowl ecology and can thus be used to aid management procedures. It is the purpose of this paper to summarize results relating to these species obtained following banding operations conducted by the Victorian Fisheries and Wildlife Department between 1952 and 1969. Results obtained for other species have been reported elsewhere (Norman 1970, 1971b).

METHODS

Black Ducks and Mountain Ducks were trapped at various localities in Victoria using baited traps similar to those described by McNally and Falconer (1953). Traps were generally set close to water, and birds when caught were transferred to holding cages. During banding birds were usually sexed and aged using cloacal examination (Hoch-

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baum 1942). Plumage characteristics also were recorded although few females were aged by this procedure.

Bands from birds found dead (recovered) were forwarded to the Fisheries and Wildlife Department. The recovery details were recorded and coded, punched on data cards, collated with banding information (see Downes 1971, for additional details) and then analysed using computer tabulations. Data discussed below relate to Black Duck banded between 1952 and 1969, and Mountain Duck banded between 1954 and 1967, which were recovered to 31 December 1969. When incomplete recovery information was received, attempts were made to elicit further details. Such information was not always obtained and hence there is variation in totals presented in the tables given below. Mortality and associated data have been calculated by methods outlined by Balham and Miers (1959), Bellrose and Chase (1950), Hickey (1952) and Reid (1966). Weighted mean annual mortality has been computed following Farner (1955) and Balham and Miers (1959).

Since 1957, samples of trapped birds were examined for the presence of shot pellets using an X-ray fluoroscope of the type described by Elder (1955) and Bellrose (1959). Whilst many birds were recaptured and examined more than once, totals given below refer only to the initial fluoroscopic examination.

RESULTS

(i) BANDING TOTALS

Between 1952 and 1969, 5644 Black Ducks were banded at 29 sites in Victoria. Of these, 3932 (69.7 per cent) were trapped during the more continuous operations conducted at Serendip, the Fisheries and Wildlife Research Station, near Geelong. Annual banding totals have varied between 5 (1963) and 1743 (1953). Of the 3798 Mountain Ducks caught at 15 localities in Victoria between 1954 and 1967, 1816 were caught at Lake Martin and 1081 at Lake Rosine, both at the northern end of Lake Corangamite near Cressy in Western Victoria. A further 474 were trapped at Serendip. Annual totals varied between nil (1953) and 1923 (1960).

(ii) SEX AND AGE TOTALS

Of the Black Ducks banded, 1980 were males, 1850 females and 1814 were released without being sexed; of those sexed 51.7 per cent were males. Table 1 gives details of annual catches made at Serendip since 1952, and since few females were aged, the adult to juvenile proportion shown has been based on capture of males only. The percentage of males in the sexed total is also given, as are the numbers of birds released without sexing.

Males comprised 53.0 per cent of the Black

TABLE 1
Annual totals of Black Ducks caught at Serendip between 1952 and 1969. Sex composition, the number of birds released without sexing, and the adult : juvenile male percentages are also given.

Year	Totals						Percent	
	<i>Caught (all groups)</i>	<i>Male</i>	<i>Female</i>	<i>Adult male</i>	<i>Juvenile male</i>	<i>Not sexed</i>	<i>Male</i>	<i>Adult male</i>
1952	443	2	1	—	1	441	66.6	—
1953	1181	335	455	234	79	371	43.8	74.8
1954	1	—	—	—	—	1	—	—
1955	34	2	3	2	—	29	40.0	100
1956	179	85	79	24	46	15	51.8	34.3
1957	205	70	59	25	4	76	54.3	86.2
1958	80	42	38	36	3	3	52.5	92.3
1959	29	13	16	—	13	—	44.8	—
1960	19	10	9	10	—	—	52.6	100
1961	79	43	36	21	12	—	54.4	63.6
1962	112	68	43	53	12	1	61.3	81.5
1963	—	—	—	—	—	—	—	—
1964	410	235	173	163	69	2	57.6	70.3
1965	369	221	140	115	106	4	61.2	52.0
1966	358	194	159	145	49	5	55.0	74.7
1967	339	185	154	76	109	—	54.6	41.1
1968	22	15	7	8	7	—	68.2	53.3
1969	72	50	22	37	13	—	69.4	74.0
<i>Totals</i>	3932	1570	1394	949	523	948	53.0	64.5

Ducks sexed at Serendip since 1952, with almost 113 males being trapped for every 100 females. Juvenile birds made up 35.5 per cent of the catch of male birds, i.e. adult to juvenile ratio of 1:0.55.

Of the 3798 Mountain Ducks processed between 1954 and 1967, 1422 were males, 2278 females and 98 were released without being sexed; of the sexed total only 38.4 per cent were males. Few females were aged at banding but the adult to juvenile male ratio was 1:0.6.

(iii) RECOVERIES

To the end of 1969, 1461 bands have been returned from recovered Black Ducks, i.e. 25.9 per cent of the banded total. Shooting was recorded as the cause of death for 1176 (80.5 per cent) of these recoveries and thus of 20.8 per cent of birds banded. Males made up 55.5 per cent of birds sexed at banding and later recovered.

For Mountain Ducks, 749 bands were returned to the end of 1969, i.e. a 19.7 per cent return for the banded total. Of the recoveries, 652 (87.1 per cent) were shot. Included in the recoveries were 317 banded as males and 404 banded as females, a recovery rate (recoveries/banded) of 22.3 per cent for males and 17.7 per cent for females.

Table 2 compares the annual banding total of Black Ducks with recoveries made within a year and to the end of 1969. On average 14.2 per cent of birds banded in any year were recovered within 12 months, and 6.6 per cent subsequently. The data show that there has been little relationship between the size of any banded cohort and its

eventual recovery rate. For Mountain Ducks, an average of 9.5 per cent were recovered within 12 months of release and 10.2 per cent subsequently.

The distribution of recoveries of Black Ducks shot on a known date within open seasons in Victoria is summarized in Table 3, where attention has been paid to totals reported for the first week of each season. Prior to 1958, season length varied from 89 days in 1952 to 62 days in 1955. However since 1958, seasons have been declared from the penultimate Saturday in February to the last in April (i.e. a length of between 63 and 71 days). The Table shows that from 1953 onwards an average of almost 40 per cent of recoveries have been made during the first week of a season, and 31 per cent on the first day of the season. For Mountain Ducks the respective figures are 34.5 and 28.5 per cent. Such figures are minimal since other recoveries were made during each season without accurate dates being provided.

(iv) DISPERSAL

Table 4 summarizes movement undertaken by Mountain and Black Ducks banded in Victoria and eventually recovered. Most recoveries of both species were made within 100 km (62.5 miles) of the banding site; 81.1 per cent of Black Ducks and 76.0 per cent of Mountain Ducks were recovered within 250 km (156.3 miles). The table also shows movements undertaken by adult and juvenile males. Whilst 57.6 per cent of juvenile Black Duck recoveries were within 100 km of the release site, only 41.8 per cent of adults were within this distance and respective figures for the 250 km

TABLE 2
Recoveries of Black Duck banded in Victoria between 1952 and 1969.

Year	Banded	Recovered			Percent Recovered	
		<i>1st year</i>	<i>Later</i>	<i>Total</i>	<i>1st year</i>	<i>Total</i>
1952	469	44	16	60	9.4	12.8
1953	1743	177	91	268	10.2	15.4
1954	231	41	13	54	17.8	23.4
1955	138	9	13	22	6.5	15.9
1956	180	32	16	48	17.8	26.7
1957	489	107	47	154	21.9	31.5
1958	112	31	7	38	27.7	33.9
1959	165	29	9	38	17.6	23.0
1960	152	30	18	48	19.7	31.6
1961	159	20	14	34	12.6	21.4
1962	158	27	14	41	17.1	26.0
1963	5	—	—	—	—	—
1964	430	73	46	119	17.0	27.7
1965	374	55	24	79	14.7	21.1
1966	406	58	25	83	14.3	20.4
1967	339	60	15	75	17.7	22.1
1968	22	4	—	4	18.2	(18.2)
1969	72	6	—	6	8.3	(8.3)
<i>Totals</i>	5644	803	368	1171	14.2	20.8

zone were 82.2 and 76.8 per cent. Young male Mountain Ducks moved less than did adults, thus 53.2 per cent of the juvenile recoveries were made within 100 km compared with 45.8 per cent of the adult male recoveries. Within 250 km of the banding site, 62.8 per cent of adult and 73.6 per cent of juvenile recoveries were made.

Fig. 1 shows the distribution of recoveries of Black Ducks banded in Victoria. The diagram also indicates the major river systems in Victoria and

shows other features relevant to recovery locations. While dispersal is clearly widespread, it is apparent that movement is eastwards into the swamps and deeper waters around the Gippsland Lakes, to the west into Western Victoria and South Australia with some birds reaching the Lake Alexandrina area. There also appears to be a broader movement with birds dispersing widely into central and northern Victoria to the tributaries of the Murray and beyond. Some birds have been recovered in

TABLE 3
Recoveries of banded Black Duck in Victoria during open seasons, 1953-1969.
(*No recoveries were made within the first week of 1952).

Year	Number Recovered			Percent of Total	
	<i>In season</i>	<i>In first week</i>	<i>On first day</i>	<i>In first week</i>	<i>On first day</i>
1953*	111	17	9	15.3	8.1
1954	84	37	31	44.1	36.9
1955	36	17	14	47.2	38.4
1956	38	24	15	63.2	39.5
1957	54	26	18	48.2	33.3
1958	118	66	59	55.9	50.0
1959	35	19	18	54.3	51.4
1960	49	25	19	51.0	38.8
1961	39	12	9	30.8	23.1
1962	39	21	17	53.9	43.6
1963	24	14	10	58.3	41.7
1964	29	9	6	31.0	20.7
1965	70	19	16	27.1	22.9
1966	78	24	21	30.8	26.9
1967	62	26	20	41.9	32.3
1968	52	20	13	38.5	25.0
1969	26	1	0	3.9	nil
<i>Totals</i>	944	377	295	39.9	31.3

TABLE 4
Recoveries of Victorian banded Black Ducks and Mountain Ducks in relation to distance from banding sites. Details are given for all recoveries and comparison is made between males banded as adults and as juveniles.

	Distances in km							
	0-50	51-100	101-150	151-200	201-250	251-300	301-400	400+
BLACK DUCK								
All sex and age groups								
Number	551	120	99	101	196	67	81	97
Percent of total	41.9	9.1	7.5	7.7	14.9	5.1	6.2	7.4
Adult males								
Number	92	27	29	25	46	15	27	24
Percent of total	32.3	9.5	10.1	8.8	16.1	5.3	9.5	8.4
Juvenile males								
Number	82	16	15	8	19	8	9	13
Percent of total	48.2	9.4	8.8	4.7	11.1	4.7	5.3	7.6
MOUNTAIN DUCK								
All sex and age groups								
Number	256	116	53	44	71	71	42	58
Percent of total	36.0	16.3	7.5	6.2	10.0	10.0	5.9	8.2
Adult males								
Number	23	4	2	2	6	11	3	8
Percent of total	39.0	6.8	3.4	3.4	10.2	18.6	5.1	13.6
Juvenile males								
Number	17	17	6	3	4	1	9	7
Percent of total	26.6	26.6	9.4	4.7	6.3	1.6	14.1	10.9



FIG. 1.—Distribution of recoveries of Black Ducks banded in Victoria between 1952 and 1969.

Tasmania (42) and northern Queensland (2) and one, banded at Serendip, was recovered 25 months later at Otago in New Zealand, a distance of about 1900 km (1200 miles).

In 1953, 1181 Black Ducks were banded at Serendip. Fig. 2 shows the recovery pattern for 597 birds banded between January and March, and Fig. 3 the corresponding pattern for 584 birds banded between April and August. Recoveries in each case have been grouped into those made in 'summer' (November to March), 'winter' (April to August) and recoveries made after March 1955. Whilst recoveries made in the first summer period were concentrated around Serendip, some birds evidently moved far between January and March 1953. Dispersal was more widespread later and there was little evidence of return movements during second and subsequent summers. First summer recoveries of birds banded between April and

August 1953 were generally away from Serendip and few recoveries were subsequently made in that area.

Fig. 4 shows the location of recoveries for Mountain Ducks banded in Victoria. Dispersal from the major banding sites (Lakes Martin and Rosine, and Serendip) has been predominantly northwards with birds being recovered widely throughout the inland plains of western and central Victoria. Many recoveries were made in the Lake Corangamite area, in the Gippsland Lakes region and around Lakes Albert and Alexandrina in South Australia and some birds (11) have also been recovered in Tasmania. But the diagram indicates that few Mountain Ducks banded anywhere in Victoria move beyond the Murray.

Fig. 5 presents recoveries of Mountain Ducks caught at Lakes Martin and Rosine during the periods January to March of 1960 and 1961 when

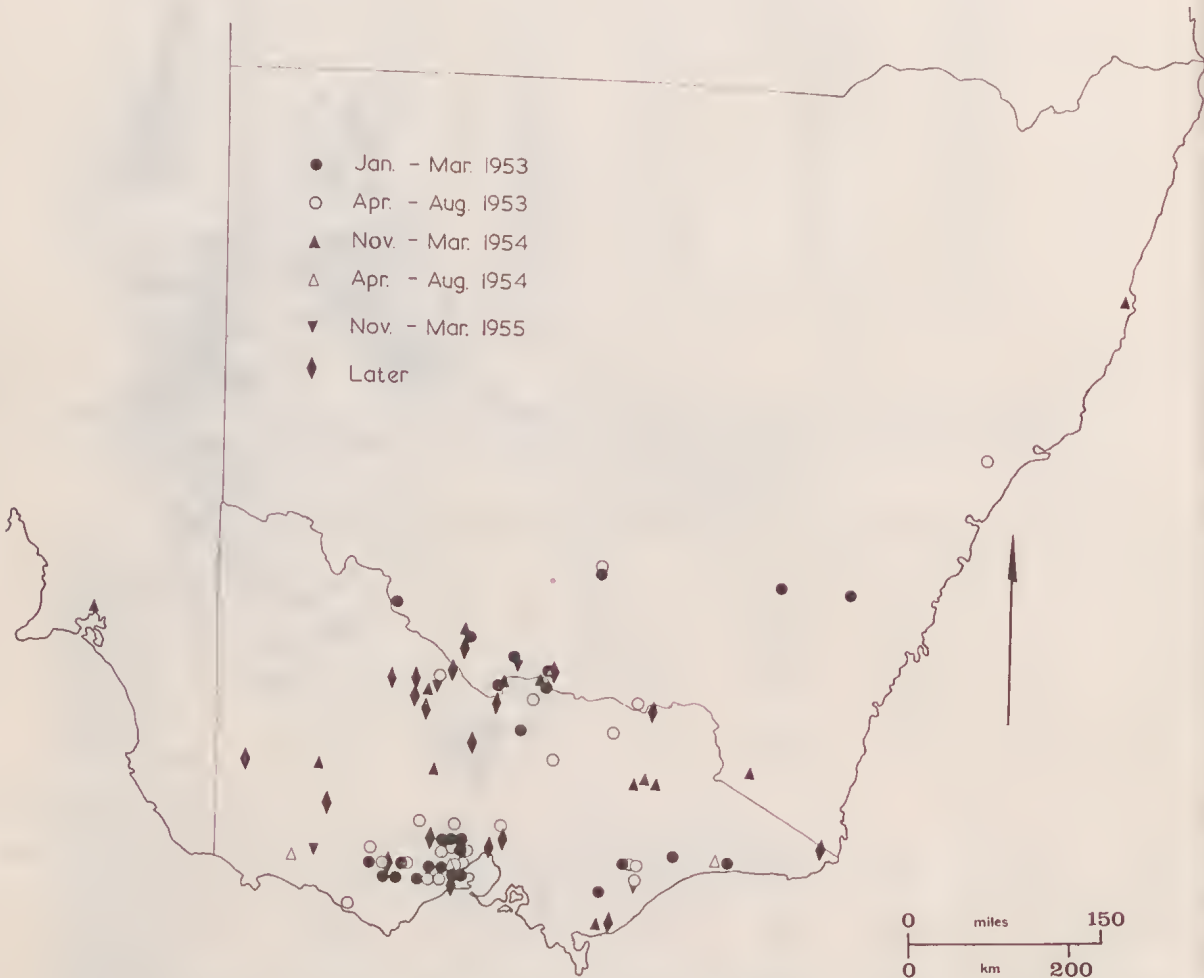


FIG. 2.—Recovery locations of Black Ducks banded at Serendip between January and March 1953.



FIG. 3—Recovery locations of Black Ducks banded at Serendip between April and August 1953, and recovered from November 1953 onwards.

2168 birds were banded. Recovery totals for birds banded at both sites have been combined, since the sites were only about a mile apart and trapping was taking place at a time when large flocks occurred. The diagram distinguishes between 'summer' and 'winter' recoveries, again in an attempt to define the source areas of the birds congregating in the Lake Corangamite region. Recoveries to the end of March, for either year of banding, show that dispersal is widespread in the summer, though some birds were recovered near the banding site in the summer and winter months.

(v) MORTALITY

Recovery totals (for shot birds only) in year classes since banding are given for both species in Table 5, as are mortality and survival data based on percentages of bands returned. In this study 67·3 per cent of the recovered Black Ducks

and 48·8 per cent of recovered Mountain Ducks were killed within a year of banding. Within four years 93·3 per cent mortality occurred in banded Black Ducks and 90·4 per cent in banded Mountain Ducks. The average mortality rate for Black Ducks in the 0·4 year period after banding was 47·4 per cent and the weighted mean mortality rate 56·7 per cent. Based on the latter figure, expectancy of life for Black Ducks of all sex and age groups was only 1·26 years post-banding. For Mountain Ducks average mortality in the four years following banding was 43·9 per cent and life expectancy 1·44 years, based on a weighted mean mortality rate of 49·1 per cent.

In Table 6, the mortality and survival data (based on weighted mortality rates) for various sex and age groups have been summarized. For both species, juvenile and female mortality is high and the corresponding life expectancy low.



FIG. 4—Distribution of recoveries of Mountain Ducks banded in Victoria between 1954 and 1967.



FIG. 5.—Recoveries of Mountain Ducks banded at Lakes Martin and Rosine between January and March in 1960 (open symbols) and 1961 (closed symbols).

TABLE 5

Recoveries, by shooting only, of Black Ducks and Mountain Ducks banded in Victoria.

	Recoveries in years following banding						
	0-1	1-2	2-3	3-4	4-5	5-6	6+
BLACK DUCK							
Total banded and available for recovery	5644	5572	5550	5211	4805	4431	4431
Total recovered	803	144	109	49	35	13	18
Percentage recovered	14.22	2.58	1.96	0.94	0.73	0.29	0.41
Mortality series	67.29	12.22	9.29	4.45	3.44	1.39	1.92
Cumulative recovery (%)	67.29	79.51	88.80	93.25	96.69	98.08	100
Survival series	32.71	20.49	11.20	7.75	3.31	1.92	nil
Mortality rate	67.3	37.4	45.3	39.7	(average 0-4 years = 47.4 % 1-4 years = 40.8 %)		
MOUNTAIN DUCK							
Total banded and available for recovery	3798	3798	3790	3785	3755	3720	3720
Total recovered	319	132	74	65	33	16	13
Percentage recovered	8.40	3.48	1.95	1.72	0.88	0.43	0.35
Mortality series	48.83	20.20	11.35	9.98	5.10	2.50	2.03
Cumulative recovery (%)	48.83	69.03	80.38	90.36	95.46	97.96	99.99
Survival series	51.17	30.97	19.62	9.64	4.54	2.03	nil
Mortality rate	48.8	39.5	36.6	50.9	(average 0-4 years = 43.9; % 1-4 years = 42.3 %)		

TABLE 6

Mortality rates of various age and sex groups of Black and Mountain Ducks banded in Victoria between 1952 and 1969, as determined from shot recoveries.

Sex and age group	Number banded	Number recovered	Average mortality			Life expectancy (years)
			(Years after banding)			
			0-1	1-4	0-4 (Mean)	
BLACK DUCK						
Juvenile male	629	158	73.5	43.5	50.8	1.09
Adult male	1096	272	57.3	48.4	50.6	1.38
All male*	2108	506	64.3	46.9	51.2	1.26
Juvenile female	303	69	75.7	35.6	45.6	1.10
All female*	2153	443	75.5	35.6	45.6	1.09
All birds†	5644	1151	67.3	40.8	47.4	1.26
MOUNTAIN DUCK						
Juvenile male	232	56	51.5	54.8	54.0	1.48
Adult male	350	63	39.7	42.3	41.7	1.68
All male*	1422	270	47.8	40.6	42.4	1.55
Juvenile female	117	27	55.4	55.7	55.6	1.25
All female*	2278	357	48.6	45.7	46.5	1.52
All birds†	3798	652	48.8	42.3	43.9	1.44

* Includes birds of unknown age.

† Includes birds of unknown sex and age.

(vi) X-RAY EXAMINATION

Results obtained during fluoroscopic examination of 2296 Black Ducks at seven localities in Victoria between 1957 and 1969 are shown in Table 7, as are data collected from 3466 Mountain Ducks examined at six sites between 1958 and 1967. Most Black Ducks (1974, 85.9 per cent) were processed at Serendip and 86.2 per cent of the Mountain Ducks were processed at Lakes Rosine and Martin: totals have therefore been pooled for each species.

Of the Black Ducks examined, 13.8 per cent

carried shotgun pellets and pellets were found in 22.3 per cent of Mountain Ducks. In both species adult males contained more pellets than did any other group. Most Black Ducks (62.3 per cent) and Mountain Ducks (55.6 per cent) carried only one pellet but a maximum of eight and 25 were recorded respectively.

(vii) SHOOTING MORTALITY AND PRODUCTION

As pointed out by Bellrose (1953, 1955) and Bellrose and Chase (1950), cripple loss, where birds are shot and die without being retrieved, and non-return of bands, affect recovery rates and

TABLE 7

Results of fluoroscopic examination of Black Ducks and Mountain Ducks trapped in Victoria between 1957 and 1969.

	Number examined			Number of pellets					
	<i>With Shot</i>	<i>Without Shot</i>	<i>Percent With Shot</i>	1	2	3	4	5	6
BLACK DUCK									
Juvenile males	19	442	4.12	14	2	2	1	—	—
Adult males	143	652	17.98	84	36	11	7	2	3
All males*	176	1112	13.66	104	41	15	10	2	4
Juvenile females	1	117	0.85	1	—	—	—	—	—
All females*	129	851	13.16	87	23	13	3	—	3
All birds†	316	1980	13.76	197	68	28	13	2	8
MOUNTAIN DUCK									
Juvenile males	29	202	12.55	20	6	1	1	—	1
Adult males	87	266	24.64	53	14	7	4	2	7
All males*	309	1022	23.21	173	55	40	18	6	17
Juvenile females	9	79	10.22	6	2	—	—	—	1
All females*	459	1665	21.61	257	94	56	21	13	18
All birds†	773	2693	22.30	430	149	96	39	19	40

* Includes birds of unknown age.

† Includes birds of unknown sex and age.

hence mortality estimates. No information is available to gauge the importance of such factors in Australia apart from that of Lavery (1969), who showed a 14 per cent loss for Black Ducks shot in Queensland, but Balham and Miers (1959) approximated a 12 per cent cripple loss and 20 per cent non-return of recovered bands in New Zealand. In Victoria a prize system (of 'lucky bands' preselected prior to the shooting season) has operated since 1958 and perhaps has maintained a fairly constant proportional rate of band return. However, as shown in Table 2, recovery rates in the year post-banding are variable and probably relate closely to local wetland conditions and waterfowl availability.

Application of Balham and Miers' estimation implies that some 27.5 per cent of banded Black Ducks and 22.6 per cent of Mountain Ducks die from shooting.

Estimates of productivity necessary to maintain population levels may be obtained from $x = Mw/50(1-M)$, where x is the number per pair, M is the first year mortality and Mw equals annual loss per 100 adults (Balham & Miers 1959). Substitution, using the more extensive data for males, shows that each Black Duck pair must raise four young, and Mountain Ducks two young, to the flying stage each year to sustain the present shooting pressure.

DISCUSSION

The distribution of recoveries of banded waterfowl is mostly dependent on habitat distribution, habitat quality and the consequent shooting, which probably is of an even density throughout south-eastern Australia. Thus the recovery locations

shown in Figs. 1 and 4 reflect general habitat requirements available to the two species.

Black Ducks banded in Victoria, particularly at Serendip, have been recovered widely in the State on river systems and the more permanent wetlands. In general dispersal has been towards the Murray and its tributaries, to Gippsland and to Western Victoria and South Australia. Movement (Table 4) has been slightly more pronounced than that recorded for the species banded elsewhere. In this study 51 per cent were recovered within 100 km of the banding site, compared with almost 69 per cent recovered in the same distance in South Australia (Norman 1971a), and Frith (1967) showed a 58 per cent recovery within 50 miles (80 km). Juvenile birds, being apparently more prone to shooting, are recovered closer to banding sites than adults. Although recoveries of Black Ducks banded in 1953 at Serendip showed that a small number resided in or around the banding area permanently, most dispersed widely after banding (Figs. 2 and 3). There was no evidence of a return movement and it is apparent that in that area 'local' birds were joined by others, moving perhaps in response to decreasing water levels (see also Ford 1958) to congregate in summer, and later disperse. Morgan (1954) showed a similar pattern at Altona, about 30 km from Serendip. Banding in Victoria and in South Australia (Norman 1971a) did not indicate a movement southwards in summer, northwards in winter, as found for birds banded in inland Australia (Frith 1963).

Mountain Ducks also increase in numbers during summer months at Altona, and it was suggested that dispersal into Western Victoria took

place in spring months (Morgan 1954). Indeed Frith (1967) suggested that Mountain Ducks in south-eastern Australia showed a regular movement with large congregations occurring in certain areas following breeding. Dispersal from such flocks, in which moulting takes place, results in birds returning to breeding areas (Frith 1967).

In the period encompassed by this study most birds were banded at summer congregations in Western Victoria and birds moved to be recovered generally northwards of the banding station, in areas where breeding is assumed to occur (Frith 1967). The distribution pattern of recoveries of Mountain Duck (Fig. 4) indicates that the species is widely dispersed throughout the central and western plains in Victoria and in the Gippsland wetland systems. It is notable that few birds were recovered in the higher eastern regions and none were obtained in the northern Mallee. Some birds apparently move from breeding sites in Tasmania to summer congregations in Victoria, since recoveries in the reverse direction have occurred. Such congregations seem to occur annually: seasonal population changes occur in the Lake Corangamite area with summer maxima and this resembles events in moulting areas elsewhere, as described by Frith. Some interchange may take place between moulting areas since it is known (H. Wright pers. comm.) that moulting takes place in the Lake Wellington area, Gippsland, and recoveries of birds banded in summer flocks in the Western District have been shot in summer near Lake Wellington. Certainly very few (two out of 1698) birds trapped in one summer period at Lakes Martin or Rosine were retrapped at the same location in the next summer.

The majority (52.3 per cent) of banded Mountain Ducks were recovered within 100 km, 66 per cent within 200 km and 86 per cent within 300 km, a result similar to that reported for Mountain Ducks banded in South Australia (Norman 1971a). Few birds banded in Victoria or South Australia moved more than 400 km, and the movements of both Black Ducks and Mountain Ducks are much more restricted than those reported for Grey Teal (Frith 1963, Norman 1971a).

Mortality rates shown in Tables 5 and 6 indicate that 67.3 per cent of recovered Black Ducks and 48.8 per cent of Mountain Ducks died within a year of banding; 93.3 per cent of Black Ducks and 90.4 per cent of banded and recovered Mountain Ducks were dead four years after banding. In South Australia Black Duck mortality was lower in the year post-banding (55.3 per cent) but within four years 95.7 per cent mortality had occurred, and life expectancy was

slightly longer (1.36 years) than that of 1.26 years recorded for Victorian banded Black Ducks (Norman 1971a). Frith (1963) presented similar data but Balham and Miers (1959) showed a 73.6 per cent mortality in the year following banding, a rate equalled in this study by juvenile males and exceeded by females (Table 6). Mean mortality was higher in the females banded in New Zealand (Balham & Miers 1959) and during this study, but Frith (1963) found that the males showed the higher mortality.

Mortality data for the Mountain Duck banded in Victoria differ from those given for birds banded in South Australia. There, although an average of 43.7 per cent mortality occurred in the four years following banding (cf. 43.6 per cent in Victoria), first year post-banding mortality was lower (43.98 per cent compared with Victorian 48.8 per cent) and life expectancy longer (1.79 years compared with 1.44 years). Although Frith (1967) stated that the Mountain Duck was not considered to be a good game species, it is clear that many are shot in Victoria.

Both absolute and relative recovery rates have been high during this study. To the end of 1969, 25.9 per cent of Black Ducks and 19.7 per cent of Mountain Ducks banded in Victoria have been recovered and of these 20.8 and 17.4 per cent were shot. By comparison Frith (1963) gave a return rate of 13.2 per cent for Black Ducks banded mainly in New South Wales. Norman (1971a) showed that 24.5 per cent of Black Ducks banded in South Australia were recovered, 21 per cent by shooting and 18.5 per cent of the Mountain Ducks banded there were recovered, 15.2 per cent by shooting. In New Zealand, Balham and Miers (1959) reported that some 34 per cent of banded Black Ducks were shot and recovered with 25.2 per cent being shot within a year of banding (cf. 14.2 per cent this study; 7.15 per cent Frith 1963).

Table 6 shows that life expectancy is greater in males and that juvenile birds undergo a greater post-banding mortality than do adults. If fluoroscopic examination results (Table 7) are representative of shooting pressure then males, which carry more shot pellets than do females, must be subject to more hunting. Juvenile birds, which have a lower life expectancy and a lower shot content than older birds may be more prone to shooting than the more experienced adults, and consequently survival (and shot content) is reduced. The difference in shot content between males and females, also found in ducks and geese in Europe and America (Elder 1950, 1953), may relate to size differences, but there may be additional mortality factors affecting female survival in

or after the breeding season, or outside the hunting season (Balham & Miers 1959, Bellrose & Chase 1950). Apart from three years (Table 1) sex ratios for Black Ducks caught at Serendip have been in favour of males, and although this could have resulted from a trapping bias (Bellrose & Chase 1950) or a higher initial proportion of males (Petrides 1944), it may relate to the higher female mortality.

Natural productivity in a stable population subjected to hunting must be sufficient to allow for this additional mortality factor, which presumably will show a proportional increase as habitat decreases through drought or drainage. Productivity estimates presented here have been based on mortality data gained from recovery of banded birds. No information is available in Victoria regarding clutch size, hatching success, or survival of young to breeding for Black Ducks or Mountain Ducks, and it is clear that a more detailed knowledge of such aspects is required for further elaboration of data. Frith (1967) considered that most Black Duck nests held 8 to 10 eggs with clutches averaging 9.1 eggs and since each pair must raise four young annually to allow mortality to continue at rates shown in this study, then reproductive efficiency must be maintained at about 44 per cent. Lavery (1970) showed that for a small sample of broods of Black Ducks in northern Queensland there was an average of 2.0 ± 1.06 in the 'old flapper' stage. Mountain Ducks usually have between 10 and 14 eggs, but variation between 5 and 22 have been reported (Frith 1967) and the production of two young each year by a pair would appear within the species' capability. For the Black Duck, no data are available regarding brood size and success. Population levels could of course be supplemented by birds moving in from other states.

Levels of productivity for a game species depend on several factors including maintenance of breeding habitats with adequate nutritional reserves, and will be affected by the extent of shooting pressure to which the species is subjected. Detailed understanding of species' ecological requirement is required if breeding or, as with Mountain Duck, moulting habitat is to be maintained. The results obtained in this study suggest that neither species is declining as a result of shooting pressure. However, it is possible that destruction of habitat may in itself increase shooting pressure. Table 3 shows, for the Black Duck, that reductions in shooting kill may be achieved by restrictions in allowable bag limits during the early part of the shooting season. Further, since both species move to some extent beyond Victoria,

maintenance of the species depends on co-operative measures at the interstate level.

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FAULTING AND THE PHYSIOGRAPHY OF THE CROYDON SUNKLAND, VICTORIA

By MICHAEL J. GARRATT*

ABSTRACT: New structural evidence for the development of the Croydon Sunkland of Central Victoria shows it to be largely if not entirely fault controlled.

INTRODUCTION

The area discussed (Fig. 1) is part of the Central Victoria Silurian-Devonian flysch belt. The present paper is the result of geological mapping of the Yan Ycan 1:63360 sheet carried out for the Geological Survey of Victoria during 1968-69.

PHYSIOGRAPHY

The broad physiographic divisions were first determined by Jutson (1911). Subsequently later workers have shown that there are three main physiographic divisions (Fig. 1): the Nillumbik Terrain (Hills 1934), the Croydon Sunkland (Juston 1911) and the Triassic Erosion Surface (Neilson 1967).

The Triassic Erosion Surface is an old erosion surface which, according to Neilson (1967, 1970), was much more extensive during the Mesozoic. It is the oldest physiographic division of the area; it has an extensive development of red soils, often more than 5 m deep, which must represent prolonged pedogenesis. The Triassic Erosion Surface ranges in height from 360 m south of Kinglake to more than 800 m on the Divide, and decreases to 125 m near Yea to the north; the average height of the surface is 600 m. The increase in elevation to 800 m is due to the resistant Mount Disappointment Granodiorite. Its southern boundary is an erosion scarp striking WNW.-ESE. from near Heathcote Junction, extending just south of Kinglake to Toolangi (Fig. 1). Hills (1959) suggested that peneplanation of the surface would have been completed by Late Triassic times.

Two eroded residuals of the Triassic Erosion Surface, the Dandenong Ranges and the upper part of the Warramate Hills, occur to the south within the Nillumbik Terrain. The western boundary only of the erosion surface of the Dandenong Ranges may have been reactivated by faulting during the Late Tertiary (Jutson 1911). This im-

plies a reversal of movement for the Montrose Monocline from east during Palaeozoic to west in Late Tertiary. Vandenberg (1971) however, stated that the present height above sea level is due to the resistance to erosion of the rhyodacites of the Mount Dandenong Volcanics Group, in particular the Ferny Creek Rhyodacite. Both models can satisfactorily explain the present configuration of the Dandenong Range.

The erosion surface of the Warramate Hills is probably a southerly extension of the Triassic Erosion Surface and occurs at an elevation of about 310 m. The soils above this level are thin; below this altitude they are thicker (up to 1 m at approx. 495485) and red like those of the Erosion Surface further north. Recognition of a residual of the Triassic Erosion Surface at this elevation demonstrates that it is warped and tilted to the south. Preservation of this surface has been aided by the resistant quartzites of the Dargile Formation, which also explains the absence of thick soil horizons above 310 m.

The Nillumbik surface was described as a peneplain by Jutson (1911) but Hills (1934) regarded it as a terrain. It had been encroaching upon the still older Triassic surface, when it was subjected to uplift and tilting and a new cycle of erosion and dissection was initiated upon it. It extends east to Healesville where it meets an extension of the Triassic Erosion Surface. Downfaulting of part of the Nillumbik Terrain on the pre-existing faults produced the Croydon Sunkland.

The Croydon Sunkland ranges in elevation from 40 m to 90 m except for two areas where the height is 155 m; these are at the 'Chirnside Estate', immediately west of Lilydale, and at 'Yerineberg', east of Coldstream. The height of the 'Chirnside' area is due to a resistant capping of Early Tertiary volcanics and sediments whilst the Yeringberg Hill owes its existence to the hardness

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of its constituent quartzites. The decrease in height of the Sunkland, the Nillumbik Terrain and the Kinglake Plateau southwards indicates regional tilting to the south. The Dandenong Creek and tributaries of the Yarra such as Steeles Creek, Woori Yallock Creek, Dixons Creek, Olinda Creek, Brushy Creek and Badgers Creek, have modified the topography of the Sunkland, but to a minor degree.

STRUCTURE

Recent work has shown that the major structural controls on the physiography of the area are faults; viz. the Yarra, Tarrawarra and Yeringberg Faults (Figs. 1 and 2) supporting the faulting hypothesis originally proposed by Jutson (1911).

(a) Yarra Fault

Originally defined by Jutson (1911) on purely physiographic grounds, its existence was rejected by later workers (Hills 1934; Gill 1940, 1942, 1949, 1965; Moore 1965). The following structural and stratigraphic evidence needs consideration in deciding whether it is a fault or not:

(i) The strike of the beds of the Dargile Formation (Thomas 1939) partly comprising the scarp (Fig. 2) differs by up to 30° from the trend of the scarp; this is especially so between Yan Yean co-ords 380570 and 300470. If the scarp were the result of erosion one might expect it to follow the strike of the hard Dargile quartzites.

(ii) An important anticlinal axis has been disrupted by the fault (Fig. 2) south-west of Yarra Glen.

(iii) Only 920 m of strata of the Dargile Formation outcrops on or adjacent to the scarp on the Yarra Glen-Christmas Hills Road compared with 1700 m in a conformable sequence in the Croydon area to the south, indicating that 800 m or so of section have been lost by faulting in the Yarra Glen area giving a minimum throw of 1300 m to the east. The presence of quartz porphyry dykes along the fault scarp north of Wonga Park and at Steeles Creek may be associated with a fault.

(iv) Displacement of strata patterns and development of local shear zones with overturned and crumpled strata were seen at Wonga Park and Yarra Glen, also suggesting the presence of a fault.

(b) The Tarrawarra Fault and Ring Dyke

This is a major EW. fault forming the northern part of the Tarrawarra Ring Dyke. Evidence of the existence of the fault is provided by the lateral displacement of both strata and fold axes (Fig. 2) in the vicinity of the River Yarra 1.6 km west

of Healesville. The fold axes become unrecognizable near the Tarrawarra Fault; contortions of the strata and limited outcrop prevent tracing of folds across the fault zone. The increased development of younger beds south of the fault, near Yarra Glen and Healesville demonstrates downthrow to the south. Its position can be located by arcuate quartz porphyry dykes north and south of the River Yarra.

(c) Yeringberg Fault:

Units within the Siluro-Devonian sequence of the Melbourne Trough are typically persistent. Sudden absence of this prominent sandstone member of the Humevale Formation 04435500 indicates a fault as shown (Fig. 2) with a downthrow to the east.

CONTROL OF PHYSIOGRAPHY

The Yarra, Yeringberg and Tarrawarra Faults are thought to have originated during the Palaeozoic. The Tarrawarra and Yarra Faults are associated with quartz porphyry intrusions thought to be contemporaneous with the Late Devonian Cribbrean and Mount Dandenong Igneous Complexes. The Yeringberg Fault, however, pre-dates the Mount Dandenong Igneous Complex because the Coldstream Rhyolites are unaffected by the fault (Fig. 2).

Late Tertiary to Early Quaternary movements (Neilson 1967, 1970) along pre-existing lines of weakness produced the Yarra scarp, caused rejuvenation of the Dandenong Ranges and thus gave rise to the Croydon Sunkland; Vandenberg (1971) has also suggested that they reactivated the Beaumaris Monocline and produced the Wheelers Hill Fault.

The Late Tertiary to Early Quaternary faulting caused widespread aggradation of the Yarra and Dandenong Creek Valleys (Fig. 1) upstream from the Wonga Park area, creating the extensive Yarra Flats of the Yarra Glen-Healesville district. Late Tertiary vertical movement along the Yarra Fault is of the order of 60 m. Patches of river alluvium have been found along the scarp between Wonga Park and Yarra Glen at least 30 m above the river's present level. The antecedent drainage pattern indicates that the displacement was slow or intermittent (Jutson 1911). This uplift caused the development of Yering Gorge, between Wonga Park and Yarra Glen, and the gorge between Warrandyte and Wonga Park.

The origin of the Brushy Creek Scarp is still undecided. Kenley (pers. comm. 1969) observed a broad zone of slickensiding and shattering at Croydon, north-east of the Maroondah Highway. Jutson (1911) proposed on physiographic grounds that the scarp was fault controlled, but Hills



FIG. 1—Physiographic divisions of Central Victoria modified from Neilson (1967).

(1934), Gill (1940, 1942, 1949, 1965), Moore (1965) and Vandenberg (1971) have maintained that it is an erosion feature only.

Vandenberg (1971) proposed that the Late Tertiary-Early Quaternary movements of the area resulted in the formation of the Wheelers Hill Fault scarp and the Beaumaris Monocline. It is probable that both faults represent reactivated Palaeozoic faults, because both the fault and monocline are in a direct line through the Brushy Creek scarp with the Yarra Fault scarp further north. It would be a remarkable coincidence if the Brushy Creek scarp were not fault controlled like these southerly extensions. Recognition of the Brushy Creek scarp as a fault scarp naturally has been equivocal, because if a fault, it would be a strike fault. All three faults mentioned above are downthrown to the east. The thickness of the Dargile Formation just south of Wonga Park is still less than the 1700 m encountered at Croydon, suggesting some loss of strata in the northern part of the scarp. The Yarra Fault intersects the Brushy Creek scarp at 60° and completely cuts out the Dargile Formation between Wonga Park and the River Yarra.

The Tarrawarra Fault, although of Palaeozoic age, has indirectly influenced the topography by restricting the outcrop of the resistant Dargile Formation south of the fault. The intersection of the ring dyke and the River Yarra both on the Yarra Glen and Healesville sides of the fault have caused the Yarra to change course (Fig. 2).

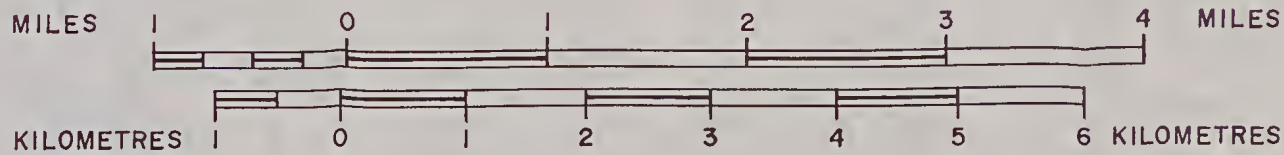
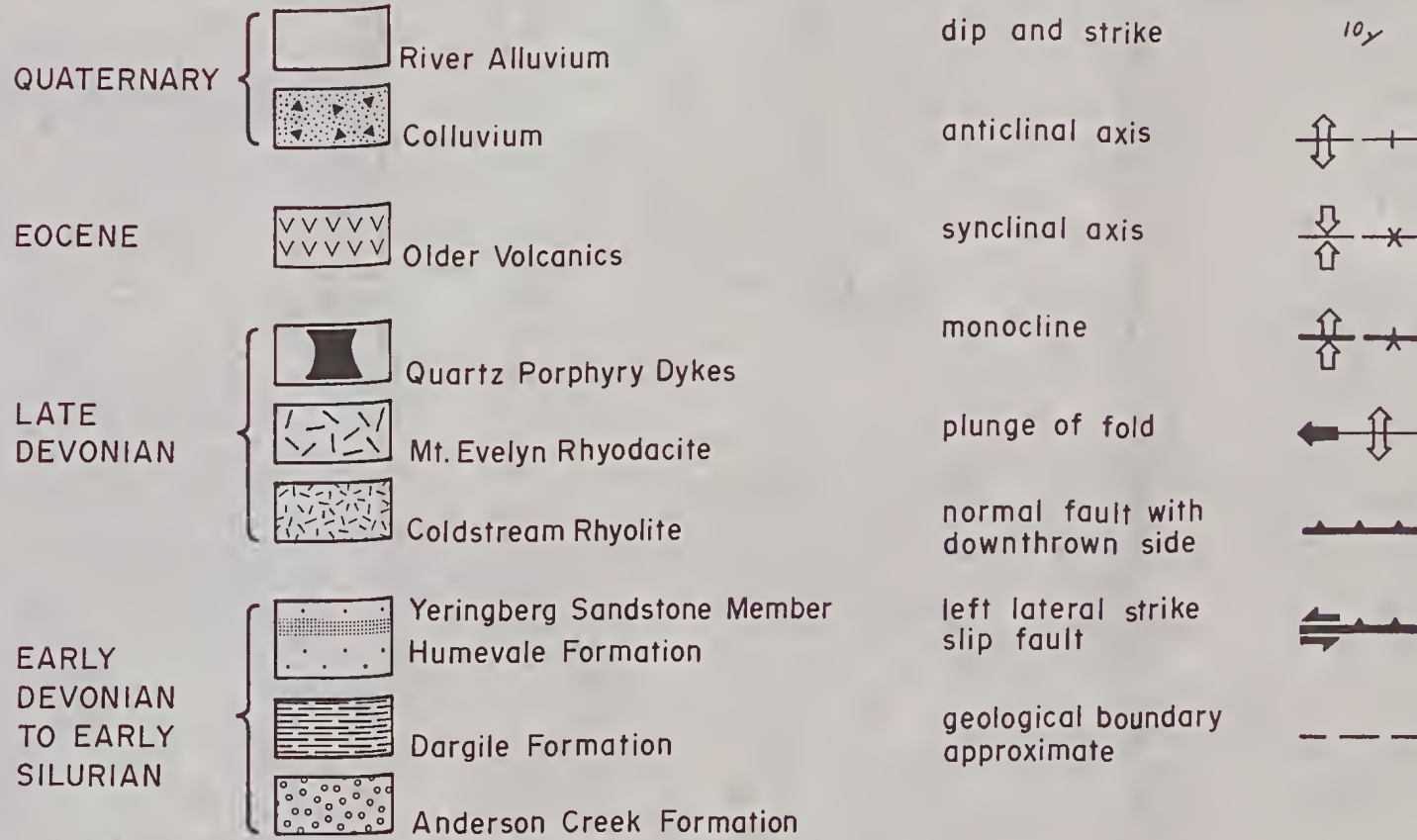
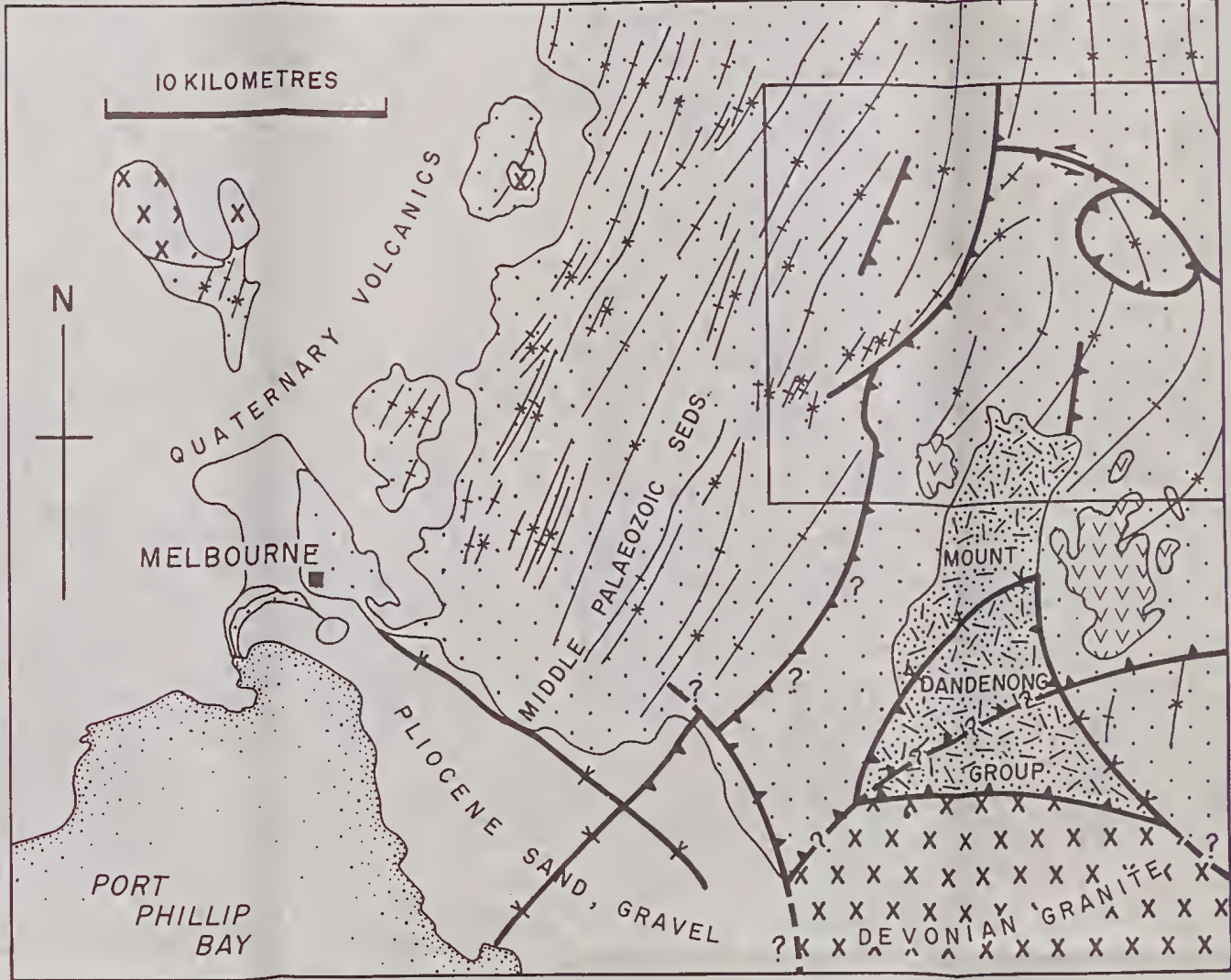
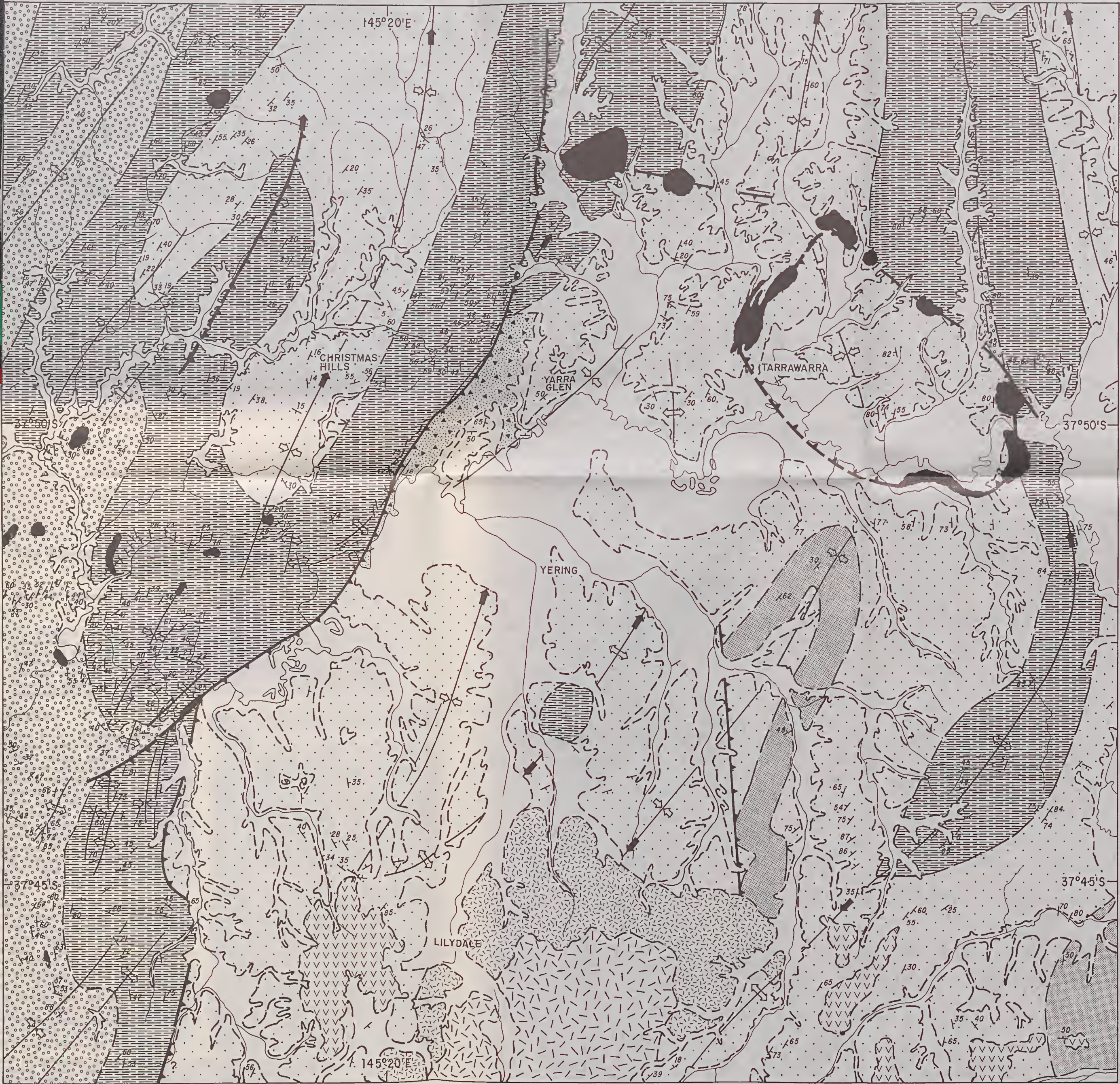
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by MJGarratt, EDGill, AVandenberg & GEWilliams from Ringwood & Yan Yean (unpub.) 1: 63 360 sheets (Geol. Surv. Vic.)

FIG. 2—Geology of the Lilydale-Yarra Glen Region, Central Victoria.

(1934), Gill (1940, 1942, 1949, 1965), Moore (1965) and Woodhouse (1971) have maintained th

Survey of Victoria, for useful discussions in earlier drafts of this paper. I am indebted to Dr. L. A

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THE BIOLOGY OF FUNGI ASSOCIATED WITH ROOT ROT OF SUBTERRANEAN CLOVER IN VICTORIA

By L. W. BURGESS¹, H. J. OGLE², J. P. EDGERTON³, L. L. STUBBS⁴ and P. E. NELSON⁵

ABSTRACT: Ecological and pathogenicity studies suggest that decline of subterranean clover pastures in Victoria is due to root rot induced by a number of fungi. Many fungi were isolated from diseased roots collected in the field. However, only *Fusarium roseum* 'Avenaceum', *Fusarium roseum* ('Sambucinum'?) and *Pythium irregulare* proved to be very pathogenic in tests with seedlings. *Fusarium oxysporum*, *Fusarium roseum* 'Culmorum' and *Fusarium roseum* 'Gibbosum' were commonly associated with diseased roots but were not very pathogenic in these particular tests.

INTRODUCTION

Subterranean clover, *Trifolium subterraneum* L., is an annual species which has become the most important pasture legume in temperate regions of southern and eastern Australia (Powell 1970). Although subterranean clover is suitable to many localities, the occurrence of patchiness or decline has been reported in Victoria (Anon. 1960), South Australia (Ludbrook, Brockwell & Riccman 1953) and Western Australia (Shipton 1967). Stand deterioration is a widespread problem in many types of pastures and the local problem will be considered in context with research carried out elsewhere on similar problems. There is at present no satisfactory review of literature on the subject.

Deterioration of stands of temperate pasture legumes are reported in England as early as 1669 and in North America as early as 1747 (Fulton & Hanson 1960). Kilpatrick and Hanson (1950) estimated losses of 39-52 per cent in first year stands of red clover, *Trifolium pratense* L., in Wisconsin while Smith (1950), also working in Wisconsin, found that 60 per cent of red clover plants that survived their first summer failed to survive their first winter and that a large proportion of those remaining died during the following summer. In Ohio, stand losses of 95 per cent in a single growing season have been reported in

individual clover fields (Selby & Thomas 1921). No estimates of losses in Australian pastures are available.

Several factors contribute to stand deterioration, but disease, particularly root and crown rot, has been a major factor (Fergus & Valleau 1926, Krcitlow & Hanson 1950, Crall 1951, Hanson 1953). In affected areas, plants are stunted and reddish-purple in colour. They may eventually die leaving a bare patch or they may recover during favourable weather. Roots of affected plants are rotted to various degrees and there is often marked discoloration of the primary root. This discoloration may extend into the crown of the plant.

Overseas, a large number of fungi has been identified on, or isolated from, affected plants (Cormack 1937a, 1937b, Buchholtz & Meredith 1938, Cherewick 1948, Staten & Leyendecker 1949, Kilpatrick & Hanson 1950, Krcitlow & Hanson 1950, Crall 1951, Hanson & Allison 1951, Hawn & Cormack 1952, Erwin 1954a, 1954b, Fulton & Hanson 1954, 1960, Kilpatrick, Hanson & Dickson 1954a, 1954b, McDonald 1955, Bushong & Gerdemann 1959, Graham & Newton 1959, Kilpatrick 1959, Leach 1959, Kainski 1960, Jenkins & Lindberg 1961, Kilpatrick & Dunn 1961, Leach, Dickason & Gross 1963, Schmitt-henner 1964, Johnson & Morgan 1965, Willis 1965, O'Rourke & Millar 1966, Aubé & Des-

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chênes 1967, Denis & Elliott 1967, Frosheiser 1967, Johnson & Keeling 1969).

Fusarium oxysporum (Schlecht.) Snyder et Hansen has generally been most frequently isolated and has been shown to cause crown and root rot of lucerne, *Medicago sativa* L. (McDonald 1955), red clover (Kreitlow & Hanson 1950, Fulton & Hanson 1954, 1960, Kilpatrick, Hansen & Dickson 1954b) and wilting of lucerne (Weimer 1928, Jenkins & Lindberg 1961, Armstrong & Armstrong 1965) and red clover (Crall 1951) as well as pre- and post-emergence damping-off of legume seedlings (McDonald 1955, Kainski 1960). However, Erwin (1954b) and Schmitthenner (1964) reported that isolates of *F. oxysporum* from lucerne were not pathogenic when reinoculated onto lucerne.

Fusarium solani (Mart.) Snyder et Hansen, another species commonly isolated from the roots of legumes showing decline symptoms, can cause severe damage to roots of red clover (Kilpatrick, Hansen & Dickson 1954b) and lucerne (Staten & Leyendecker 1949, McDonald 1955). *F. solani* also caused reductions in stands of red clover (Crall 1951).

Forms of *F. roseum* (Link) Snyder et Hansen have also been frequently isolated from diseased legumes and have been reported to be very pathogenic to seedlings (Erwin 1954a, McDonald 1955, Graham, Sprague & Robinson 1957, Kainski 1960) but not to plants beyond the seedling stage. However, Cormack (1937b) and Hawn and Cormack (1952) reported that *F. roseum* 'Avenaceum' was one of the most pathogenic species they tested. Similarly, Hawn and Cormack (1952) and McDonald (1955) found *F. roseum* 'Gibbosum', their most frequently isolated species, very pathogenic, although Cormack (1937b) considered it only weakly parasitic.

A number of other species of *Fusarium* have been isolated from roots and crowns of diseased legume plants. *F. moniliforme* (Sheld.) Snyder et Hansen caused reductions in stands of red clover (Crall 1951). *F. tricinctum* (Corda) Snyder et Hansen was the only species isolated from rotted lucerne roots by Lukezic, Bloom and Carroll (1969). It can cause complete wilting and death of several legume species and varieties within 72 hours of inoculation (Bolton & Nuttall 1968). Cormack (1937b) reported that *F. tricinctum* usually behaved as a weak pathogen on lucerne. *F. episphaeria* (Tode) Snyder et Hansen has also been reported associated with rotting lucerne roots (McDonald 1955).

A number of other fungi, such as *Rhizoctonia solani* Kuehn, *Gliocladium roseum* (Link) Thom, *Cylindrocarpon* spp. and species of *Pythium* and

Phytophthora have been isolated from the roots and crowns of pasture legumes. *R. solani* is among the most important seedling pathogens of lucerne, causing pre- and post-emergence damping-off (McDonald 1955, Graham, Sprague & Robinson 1957, Schmitthenner 1964) as well as collar rot and crown bud rot (Cherewick 1948, Hanson & Allison 1951, Hawn & Cormack 1952, Benedict 1954, Kilpatrick, Hansen & Dickson 1954a, McDonald 1955). *G. roseum* can cause severe stunting but did not kill many plants in the pathogenicity tests reported by Kilpatrick, Hansen and Dickson (1954b). The pathogenicity of species of *Cylindrocarpon* to a number of species of legume was studied by Cormack (1937a) who found that *C. ehrenbergi* Wr. was decidedly more pathogenic than any other species tested. Species of *Pythium* generally cause damping-off of seedlings and do not attack advanced plants (Buchholz & Meredith 1938, Halpin, Hansen & Dickson 1952, 1954, Erwin 1954a, Kilpatrick, Hansen & Dickson 1954b, Halpin & Hansen 1958, Schmitthenner 1964). Species of *Phytophthora* cause either seedling damping-off (McDonald 1955, Johnson & Morgan 1968, Johnson & Keeling 1969) or root rot (Erwin 1954b), Bushong & Gerdemann 1959, Froshieser 1967).

There are some Australian reports on decline of pastures associated with the presence of various root-rotting fungi. In Western Australia, *F. oxysporum*, followed by *F. roseum* 'Avenaceum' were the organisms isolated most frequently from roots of diseased subterranean clover plants (Shipton 1967). These species, as well as *F. moniliforme*, were pathogenic to sterile seedlings grown in test tubes. *F. oxysporum* has recently been reported as the cause of lucerne decline in Western Australia (Marclay 1970). In South Australia, *R. solani*, *Pythium* spp., *Ophiobolus graminis* Sacc., *Corticium praticola* Kotila, *Helminthosporium* spp. and *Fusarium* spp. were among 300 isolates from rotted roots of subterranean clover plants from 'bare patch areas' (Ludbrook, Brockwell & Riceman 1953). However, only *R. solani* produced symptoms similar to those found in the field. In Victoria, *Fusarium* spp. and *Rhizoctonia* sp. were consistently isolated from diseased plants and laboratory tests indicated that the *Fusarium* spp. were responsible for the condition (Anon 1960). Recently, Kellock (1972) reported the isolation of *F. avenaceum* from both rotted roots and seeds of subterranean clover, and demonstrated that the fungus was highly pathogenic. Decline and establishment problems associated with root rots caused by species of *Pythium* and *Phytophthora* have also been reported (Teakle 1956, Andrew 1963, Purss 1965).

A wide range in the pathogenicity of isolates of many species has been reported (Cormack 1937a, 1937b, Benedict 1954, Kilpatrick, Hanson & Dickson 1954b, Fulton & Hanson 1960, Schmitt-henner 1964, Denis & Elliott 1967). Furthermore, the relative importance of each species in the field is affected by the age of the stand, soil type, soil moisture and temperature (Cormack 1937a, 1937b, Kilpatrick, Hanson & Dickson 1954a, McDonald 1955, Graham, Sprague & Robinson 1957, Halpin & Hanson 1958, McGlohon 1959, Fulton & Hanson 1960, Kainski 1960, Willis 1965, Aubé & Deschênes 1967). Some authors have suggested that the fungi isolated from root rot lesions on legumes are weak parasites which become important only when the plants have been predisposed to infection by loss of food reserves with age, during the winter or with grazing (Young 1924, Fulton & Hanson 1954, O'Rourke & Millar 1966, Shipton 1967). Others have shown that the severity of root and crown rots is correlated with damage to roots by insects, such as the clover root borer, *Sitonia hispidula* (Fab.) (Graham & Newton 1959, Kilpatrick & Dunn 1961, Leach, Dickason & Gross 1963) and have suggested that mechanical injury to the roots due to the insects feeding facilitates the entry of the fungi. However, no direct correlation was found between *Pratylenchus* injury and root rot incidence (Leach, Dickason & Gross 1963). Furthermore, Chi, Childers and Hanson (1964) and Cormack (1937b) reported that *Fusarium* spp. can penetrate the roots of pasture legumes directly and do not require wounds for entry. Thus, the role of insect injury in the development of root rots of pasture legumes is uncertain. More recently, Khan and Banfield (1971) have suggested that failure of red clover in Massachusetts results from an interaction between red clover roots and certain viruses, *Fusarium* spp. and some insects.

The investigation reported in this paper was made to study the fungi associated with root rot of subterranean clover in Victoria and their pathogenicity.

FIELD SYMPTOMS

In the field plants affected by root rot were generally stunted and their foliage was usually reddish-purple to reddish-brown in colour. Root systems were rotted to various degrees and brown to black lesions could be observed at the junction of the lateral and tap root, along the lateral roots and at the root tip (Pl. 1 A, B, C). There was often a marked discoloration (usually reddish-brown) of the stele of affected lateral and tap roots. This discoloration frequently extended into the crown (Pl. 1, C). The affected root systems

were often completely necrotic and it was not unusual to see lateral root proliferation from the tap root immediately beneath the crown on plants where the tap root was entirely rotted (Pl. 1, B).

Similar symptoms have been observed in young subterranean clover seedlings which were damping-off (Pl. 1, D). Diseased seedlings may also have a 'water-soaked' appearance which may be accompanied by a light brown discoloration of the cortical tissues of the root.

EXPERIMENTAL METHODS

(1) Isolations from diseased roots

Diseased root systems of subterranean clover plants were carefully removed from the soil and taken to the laboratory where they were washed and cultured on various media. The roots were carefully examined before culturing and notes were taken of disease symptoms. Approximately half were surface sterilized before culturing (1-2 min. in 0.1 per cent mercuric chloride in 10 per cent ethyl alcohol followed by four washings in sterile water) and all roots were 'damp-dried' between sterile paper tissues before culturing. The majority of the root systems were sampled from the Mt. Derrimut Field Station of the University of Melbourne. The remainder were sampled from various areas in northern and north-western Victoria. The origin of each sample was recorded using the co-ordinates of a 1:100,000 map of the series based on the Australian Map Grid.

(2) Baiting method

Diseased subterranean clover roots collected at Mt. Derrimut were washed, ground in a Waring blender and mixed with a pasteurised potting mix to give approximately 5 per cent inoculum by volume. Twenty-five *Rhizobium*-treated Bacchus Marsh subterranean clover seeds were then planted in pots containing the inoculated soil. Six pots were kept at each of the temperatures 10, 15, 20 and 25°C in a CSIRO unit phytotron (type B cabinets). Two pots were removed from each temperature so that a sampling was carried out when 50 per cent of the seedlings had emerged, when 50 per cent of the seedlings had the first trifoliate leaf unfolded and at 10 days after the second sampling.

At each sampling, the seedlings were removed from the two pots and bulked. Six seedlings were selected at random for serial culturing. The root systems were thoroughly washed under a tap water spray and then washed in five changes of sterile water. Segments 2 mm long were removed from the root cap, 1 cm above the root cap, 2 cm above the root cap, half way up the root and 1 cm below the soil surface. These

were then plated serially on three media—potato dextrose agar (PDA), a selective medium for *Fusarium* (Tousoun & Nelson 1968) and a selective medium for *Pythium* and *Phytophthora* (Tsao & Ocana 1969) so that two roots were cultured on each medium. The plates were incubated at room temperature and each colony that developed was subcultured on a PDA slope for subsequent identification.

(3) Technique for soil *Fusarium* analyses

All plant material was removed and the soil sample was then ground in a mortar and pestle. A 1 gm sub-sample was placed in 100 ml of sterile 0.1 per cent water agar. The soil suspension was shaken for 1 hour before the final dilutions to 1:500 to 1:3,000 were made. One ml of the final dilution was spread evenly over the surface of approximately 25 ml of the selective medium for *Fusarium* in 90 x 15 mm Petri dishes. Ten plates were made for each dilution of each soil sample. The medium was prepared so there was time for the plates to dry for 4-5 days before use. If this was not done, bacterial contamination became severe. The plates were incubated at room temperature (20°C) for 4-7 days. The dilution which gave a good, even distribution of colonies on the plates was kept. Each colony type on these plates was then numbered and the number of colonies of that type counted and recorded. Single conidium cultures were made from a single colony of each type before the final identification was made. The estimate of the number of propagules per gram of soil was made from the colony counts.

(4) Pathogenicity tests

The isolates used in the pathogenicity tests were representatives of the following species: *F. roseum* 'Avenaceum', *F. roseum* 'Culmorum', *F. roseum* ('Sambucinum?'), *F. roseum*, *F. oxysporum*, *F. solani*, *Pythium irregulare* Buisman, *Pythium aquatile* Hohnk, *Rhizoctonia* sp. The isolates were from subterranean clover roots with the exception of *F. solani* which was isolated from soil. The roots and soil were obtained from Field 8 at Mt. Derrimut.

The *Fusarium* isolates were maintained on PDA slopes using single conidium transfers. The other species were also maintained on PDA slopes and transferred by hyphal tips. All cultures were incubated at room temperature (25 ± 4°C) in diffuse daylight.

Inoculum was prepared by growing the fungi on a sand-chaff-maizemeal medium in preserving jars (Fowler No. 31) of 800 ml capacity. The medium in each jar consisted of 250 cc (approximately 400 g) of fine sand, 250 cc of cereal

chaff containing approximately 5 per cent oat grain and 0.5 per cent wheat grain and 12 g of maizemeal. Each jar was shaken thoroughly to mix the contents before 125 ml of distilled water were added. Stainless steel lids, with 9 holes 0.5 cm in diameter, were used to permit aeration but at the same time limit drying through evaporation. To prevent contamination a layer of cotton wool enveloped in cotton gauze was placed over the lid of each jar and held down by the heat-resistant rubber rings supplied with the jars. The medium was autoclaved at 15 p.s.i. for 30 min. *Fusarium* isolates were added to the cooled medium as spore suspensions and the other species as 1 cm squares (4 per jar) of young colonies growing on PDA in Petri dishes. After inoculation, the jars were incubated at room temperature for 20 days. The daily maximum and minimum temperatures during this time were within the range 20-28°C. The inoculum was then used to amend soil (pasteurised by steam-air treatment for 30 min. at 82°C) in the ratio 4:1 (soil: inoculum) by volume. The control soil was amended with inoculum which had been exposed to propylene oxide. This involved the addition of 4 cc of propylene oxide (cooled to 0°C) to each jar of inoculum which was then sealed for 24 hours. These jars were opened for a further 24 hours in a fume cupboard for the gas to dissipate.

The soil used (pH 5) was collected from the top 15 cm of Field 8 at Mt. Derrimut. As it was heavy textured, it required breaking up in a soil shredder and moistening with a fine spray of water before pasteurising.

The amended soil was weighed into plastic buckets (17 cm tapering to 14 cm in diameter and 15 cm deep) and inoculated with a clover strain of *Rhizobium*. Three replicate buckets were used. Fifty seeds of Mt. Barker subterranean clover were sown in each bucket at a depth of 1 cm using a template. The moisture content of the amended soil was adjusted to field capacity after sowing and maintained at that level during the test. The buckets were kept in a cooled glasshouse and located at random on the benches. Glasshouse air temperatures during the test were within the range 15-30°C and soil temperatures in the root zone were in the range 17-30°C.

Twenty days after sowing, the plants were carefully removed from the soil and washed under a fine mist spray. Each plant was then rated for the degree of damage to its root system and hypocotyl according to a zero to five index scale as follows:

0—no visible lesions on roots

1—one or two small lesions (less than 0.5

cm long) on tap root or laterals, including root tip necrosis

2—more necrosis than 1 but less than 3

3—more than 2 healthy laterals above necrotic section of tap root but at least half the lower tap root with extensive necrosis

4—severe root damage—only 1 or 2 healthy laterals above necrotic section of tap root;

5—plant dead or tap root completely necrotic

The mean of the ratings of all plants in a pot was taken as the disease severity estimate for that pot. Representative necrotic roots from the various pathogenicity tests were cultured to determine the fungi present.

RESULTS

The following fungi were isolated from diseased subterranean clover roots: *F. moniliforme*, *F. oxysporum*, *F. roseum*, *F. roseum* 'Avenaceum', *F. roseum* 'Culmorum', *F. roseum* 'Gibbosum', *F. roseum* 'Graminearum', *F. solani*, *F. tricinatum*, *Cylindrocarpon* spp., *Gliocladium* spp., *Helminthosporium* sp., *Mortierella* sp., *P. irregulare*, *P. aquatile*, *Pythium* sp., *Rhizoctonia* sp. and other unidentified genera. The relative frequency of isolation of these fungi is listed in Table 1.

The species of fungi isolated from 'bait' roots of subterranean clover seedlings grown in pasteurised soil amended with naturally infected clover roots are recorded in Table 2. On the selective medium for *Phytophthora* and *Pythium*, *P. irregulare* was predominant. The less frequently isolated species were not identified to species level.

The species of *Fusarium* isolated from the soil samples taken under subterranean clover stands and the estimated number of propagules per gram of soil of each are given in Table 3.

The relative severity of root rot in Mt. Barker subterranean clover seedlings caused by the *Fusarium* spp. tested is shown in Fig. 1. Species causing root rot induced localized or spreading lesions, brown to black in colour. Affected cortical tissue frequently developed a water-soaked appearance before becoming brown to black in colour. The stele of affected roots was usually darkened with a reddish-brown discoloration similar to that in rotted roots collected in the field. The cotyledons and leaves on severely affected seedlings wilted rapidly following collapse of the root system.

The symptoms resulting from infection by *Pythium* were similar to those described above. This fungus, however, did not seem to induce the discoloration of the stele. The data on symptom severity from the tests involving *Pythium* spp. and *Rhizoctonia* sp. are given in Fig. 2.

TABLE 1

Relative frequency of isolation of fungi from diseased subterranean clover roots

Species	Relative frequency of isolation
<i>Fusarium moniliforme</i>	+
<i>F. oxysporum</i>	+++
<i>F. roseum</i>	++
<i>F. roseum</i> 'Avenaceum'	+
<i>F. roseum</i> 'Culmorum'	+++
<i>F. roseum</i> 'Gibbosum'	++
<i>F. roseum</i> 'Graminearum'	+
<i>F. solani</i>	+
<i>F. tricinatum</i>	+
<i>Cylindrocarpon</i> spp.	+
<i>Gliocladium</i> spp.	+
<i>Helminthosporium</i> sp.	+
<i>Mortierella</i> sp.	+
<i>Pythium</i> spp.	+
<i>P. irregulare</i>	+++
<i>P. aquatile</i>	+
<i>Rhizoctonia</i> sp.	+

* An arbitrary scale: + indicates occasional isolation; ++ indicates regular isolation in low numbers; +++ indicates frequent isolation.

TABLE 2

Species of fungi isolated from 'bait' roots of subterranean clover seedlings grown at four temperatures in pasteurised soil, amended with diseased subterranean clover roots

Soil Temperature °C	Isolation Medium	
	Potato dextrose agar	Selective medium for <i>Fusaria</i>
25	<i>F. oxysporum</i> (2)*	<i>F. oxysporum</i> (1)
	<i>F. roseum</i> (6)**	<i>F. roseum</i> (3)
	<i>F. roseum</i>	<i>F. roseum</i>
	'Avenaceum' (2)	'Avenaceum' (3)
	<i>Dendrodochium</i> sp. (1)	<i>Dendrodochium</i> sp. (2)
20	<i>F. roseum</i> (2)	<i>F. oxysporum</i> (1)
	<i>F. roseum</i>	<i>F. roseum</i> (3)
	'Avenaceum' (3)	<i>F. roseum</i>
	<i>Cylindrocarpon</i> sp. (1)	'Avenaceum' (1)
	<i>Dendrodochium</i> sp. (1)	<i>Cylindrocarpon</i> sp. (3)
15	<i>F. roseum</i> (1)	<i>Dendrodochium</i> sp. (1)
	<i>Torula</i> sp. (1)	<i>F. roseum</i> (2)
		<i>F. roseum</i>
		'Avenaceum' (1)
		<i>Cylindrocarpon</i> sp. (1)
10	<i>Torula</i> sp. (1)	<i>F. roseum</i> (2)
		<i>Cylindrocarpon</i> sp. (1)
		<i>Dendrodochium</i> sp. (1)

* Number in parenthesis is the total of the colonies of the fungus isolated at three sampling times from all root segments.

** Includes 'Culmorum', 'Gibbosum' and other types.

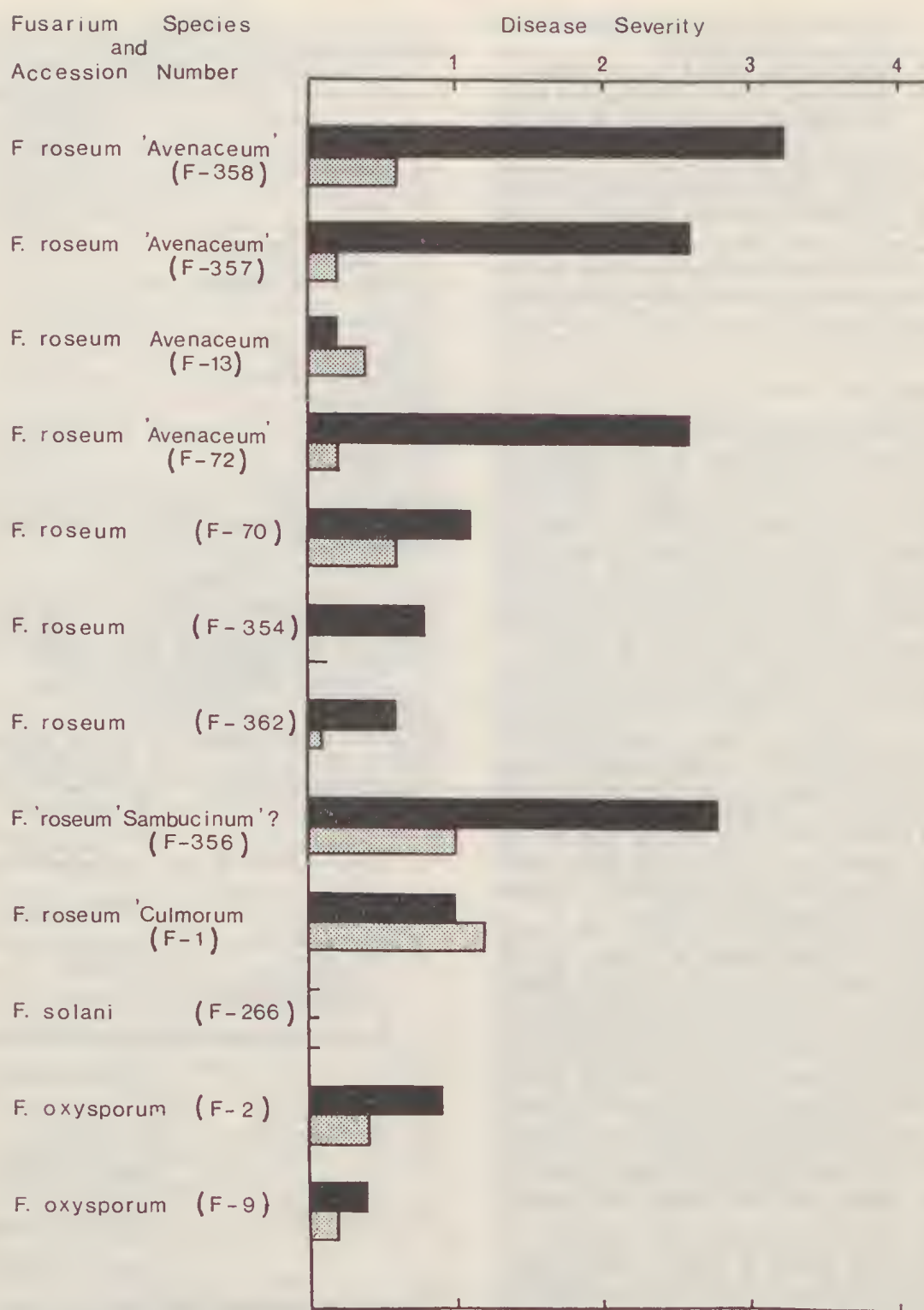


FIG. 1.—The relative severity of root rot of Mt. Barker subterranean clover seedlings caused by species of *Fusarium*, based on an arbitrary disease severity scale of 0 — 5; 0 = no visible lesions on roots; 5 = completely necrotic tap-root. Black bars—inoculated; hatched bars—uninoculated.

TABLE 3

Fusarium spp. isolated from soil samples taken under subterranean clover stands in Victoria. (Number of propagules per gram of soil $\times 10^3$)

Soil sample number	Map Reference	<i>F. oxysporum</i>	<i>F. solani</i>	<i>F. episphaeria</i>	<i>F. moniliforme</i>	<i>F. roseum</i>	<i>F. roseum</i> 'Gibbosum'
70-7-1 V	7822	8.5†	1.0				0.5
* 70-7-3 V	7822	17.0		0.5			
† 70-7-4 V	7822	5.0	1.0				
70-7-6 V	7822	5.0	0.5				
† 70-7-7 V	7822	5.0				0.5	
70-7-8 V	7822	6.5	0.5		0.5		
† 70-7-9 V	7822	3.5			2.0		1.0
† 70-7-10 V	7822	9.0			0.5		0.5
† 70-8-19 V	7124	8.0			0.5		
† 70-8-23 V	7124	7.0	1.0				
† 70-8-30 V	7925	3.0			3.5		1.4
† 70-8-31 V	7225	8.0	2.0				
70-8-32 V	7225	0.5	0.5				0.5
70-8-33 V	7925	15.5	4.0				
† 70-8-36 V	7724	0.5					
† 70-8-37 V	7823	1.0					0.5

* Samples which are bracketed are from adjacent areas within 500 ft of each other.

† Estimated number of propagules per gram of soil $\times 10^3$.

‡ Soil from areas where root rot of subterranean clover is known to occur.

DISCUSSION

The symptoms of root rot of subterranean clover observed in various areas of Victoria were similar to those described in Western Australia (Shipton 1967) and indeed similar to those shown by root rot affected temperate legumes in other countries. The species of fungi isolated from diseased roots correspond to those reported previously.

F. oxysporum was frequently isolated from diseased roots and soil. However, it was not commonly isolated from the clover seedling roots used as baits. Furthermore, isolates of *F. oxysporum* were less pathogenic than previous reports suggested (Kilpatrick, Hanson & Dickson 1954a, McDonald 1955, Anon. 1960, Kainski 1960, Shipton 1967, Marcle 1970). These observations suggest that it is a secondary invader of diseased roots. Thus, the 'bait' technique used in this study offers a possible method for differentiating primary from secondary invaders before time-consuming pathogenicity tests are undertaken.

F. solani also proved less pathogenic than ex-

pected from previous reports (Crall 1951, Kilpatrick, Hanson & Dickson 1954a, 1954b, McDonald 1955, Kainski 1960) and is probably also only a secondary invader.

Isolates of *F. roseum* 'Avenaceum' were generally most pathogenic. This is in accord with the findings of Cormack (1937b), Hawn and Cormack (1952) and Kellock (1972). It is interesting that although *F. roseum* 'Avenaceum' was not commonly isolated from diseased roots from the field or from soil, it was consistently isolated using the 'bait' technique. This suggests that it may be a primary pathogen which is not easily isolated on culture media in competition with other fungi. The development of an improved direct isolation procedure for this fungus would greatly facilitate the study of its distribution in pasture soils.

Other *F. roseum* types were frequently isolated from diseased roots and from 'bait' roots which indicates that they may also be primary pathogens. An isolate of *F. roseum* ('Sambucinum?') was quite pathogenic. *F. roseum* 'Culmorum' was not as pathogenic as expected from the results reported by Cormack (1937b). He did, however, observe that the pathogenic activity of *F. roseum* 'Culmorum' was suppressed at lower temperatures. This may account for its non-pathogenicity in our tests.

The fact that *P. irregulare* was frequently isolated from 'bait' roots suggested that it, too, is a primary pathogen. The pathogenicity studies indicated that it can cause significant root rot and damping-off of subterranean clover seedlings. It was frequently isolated from diseased roots (from both mature and immature plants) from the field and particularly from small lesions along young lateral roots and at the root tips. Thus, *P. irregulare* may have a detrimental effect on the growth of the plants through necrosis of the feeder rootlets as discussed by Wilhelm (1959).

Rhizoctonia sp. was not significantly pathogenic, in contrast to the results reported previously (Ludbrook, Brockwell & Riceman 1953, Benedict 1954, McDonald 1955, Kainski 1960). However, only one isolate was tested and it is well known that *Rhizoctonia* isolates vary in pathogenicity (Benedict 1954, Kainski 1960). The status of the remaining species as pathogens is uncertain but their low overall frequency of isolation using the three procedures suggests that they are not important.

Our results suggest that root rot of subterranean clover is caused by a complex of pathogens, since we have shown that three species representing two genera are strongly pathogenic. At this stage, not enough is known about the relative roles of these fungi or of possible interactions between them for

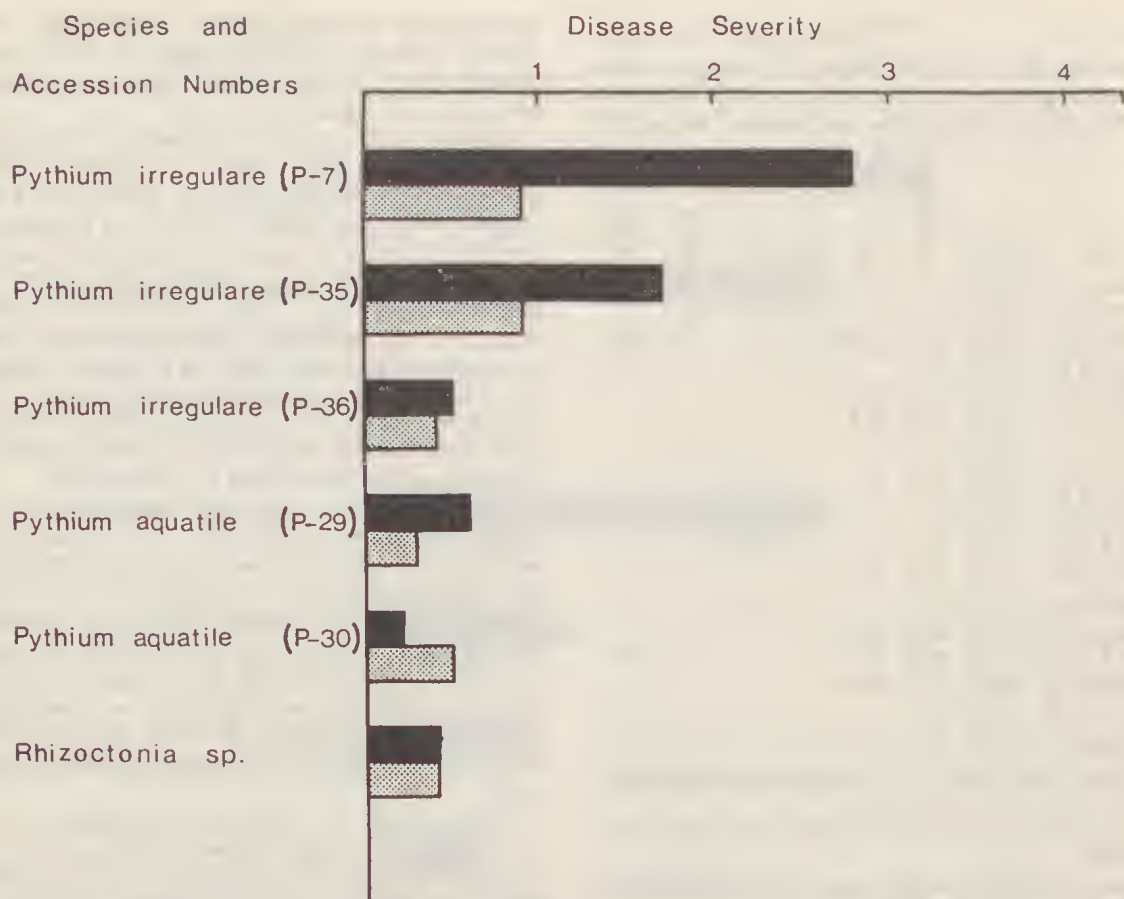


FIG. 2.—The relative severity of root rot of Mt. Barker subterranean clover seedlings caused by species of *Pythium* and a *Rhizoctonia* sp., based on an arbitrary disease severity scale of 0 — 5; 0 = no visible lesions on roots; 5 = completely necrotic tap-root. Black bars—inoculated; hatched bars—uninoculated.

any definite conclusions to be drawn as to their relative importance as pathogens.

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DESCRIPTION OF PLATE 1

Subterranean clover roots with typical root-rot symptoms. A. Rotted tap root. B. Rotted tap root with lateral root proliferation above the rotted section. C. Tap roots, with root rot, sectioned longitudinally. D. Seedlings severely affected with root rot.



DISJUNCTIONS IN THE DISTRIBUTION OF *EUCALYPTUS* SPECIES BETWEEN WESTERN VICTORIA AND THE MOUNT LOFTY-FLINDERS RANGES AREA, SOUTH AUSTRALIA

By R. F. PARSONS*

ABSTRACT: Apart from riverine and Mallee species, all eucalypts shared by Western Victoria and South Australia show range disjunctions partly related to present day low rainfall in the area between the south-east of South Australia and the Mount Lofty Ranges. All that is needed to provide habitats for continuous distributions in the past for species from coastal lowlands is higher effective rainfall or possibly lower sea-levels. It is much harder to envisage migration routes for species absent from coastal lowlands. For example, the past migration of *Eucalyptus microcarpa* to the Mount Lofty Ranges may have depended on more extensive occurrences of heavy-textured soils in the past. The disjunctions of *E. goniocalyx*, *E. Macrorhyncha* and *E. rubida* are even more difficult to explain as they are absent from coastal lowlands and inland plains at present. A possible migration route for the former two along ridges of Diapur Sandstone is suggested, while *E. rubida*, on which further work is needed, appears to have the most anomalous distribution of all.

INTRODUCTION

Recent distribution maps of South Australian tree species (Boomsma 1972) show many large disjunctions in the ranges of *Eucalyptus* species. A disjunction is said to occur when two populations of a species are more widely separated than its normal dispersal capacity (Cain 1944). For the eucalypts considered here, with no special adaptations for seed dispersal, seeds may be most unlikely to travel distances greater than twice tree height (Cunningham 1960). Although work is badly needed on whether occasional long distance dispersal can occur, the large number of disjunctions exceeding 100 km noted here suggest that the disjunct occurrences may be remnants of former continuous distributions and so be related to past regimes of climate and sea level. Such relationships are discussed with particular reference to the eucalypts of southern South Australia. Although most of the distribution data are readily available in Boomsma (1972), a discussion of possible past migration routes also requires detailed habitat data for the species concerned. These have been obtained from the author's field observations and from the literature. Because the eucalypts being dealt with are from sub-generic groups with centres of species diversity in Victoria

and New South Wales, it is possible that migration has been mainly from these states into South Australia rather than vice versa. Nomenclature follows Boomsma (1972) except that *E. viminalis* and *E. huberana* are treated together as *E. viminalis* complex. It should be noted that Boomsma (1972) may consider *E. albens* and *E. microcarpa* together under the name *E. microcarpa*.

THE DISTRIBUTIONS

Many Mallee eucalypts show more or less continuous distributions from western Victoria to drier parts of the Mount Lofty Ranges and beyond, and riverine species like *Eucalyptus camaldulensis* and *E. largiflorens* may bridge the same area fairly completely along the Murray River (Boomsma 1972). Of the remaining eucalypts in western Victoria (i.e. those from the wetter woodland areas), not one species reaches the Mount Lofty-Flinders Ranges area without a major disjunction in its distribution. In terms of the present environment, this is probably partly correlated with the fact that only three small areas in South Australia have mean annual rainfalls exceeding 700 mm; the south-eastern extremity, a part of the Mount Lofty Ranges, and western Kangaroo Island (Fig. 1).

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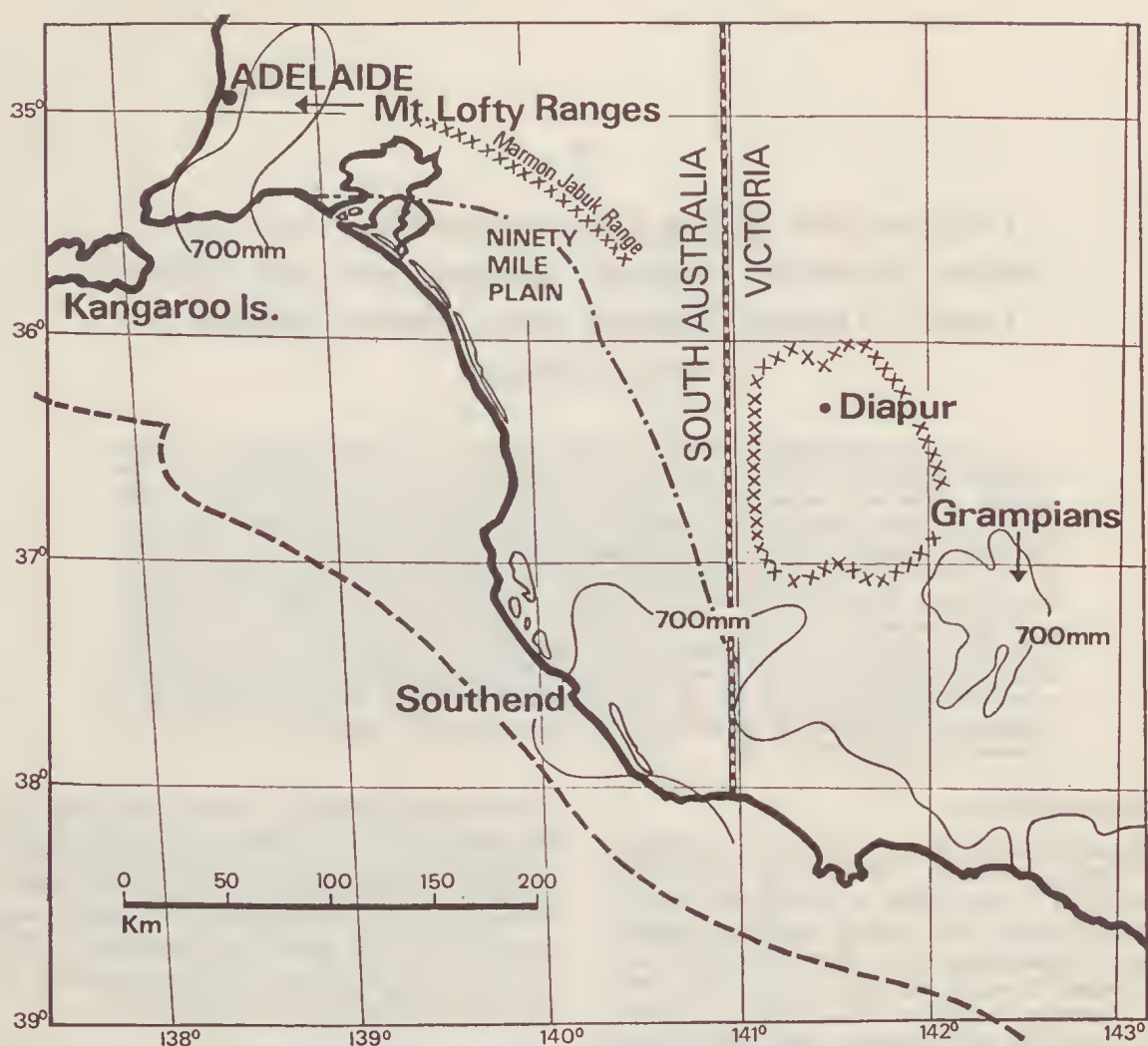


FIG. 1—The area from Western Victoria to the Mount Lofty Ranges showing place names mentioned in the text, the 700 mm mean annual rainfall isohyet, the approximate location of the southern Australian coastline during the Last Glacial (dashed line) when sea level was probably about 120 m below present, the inland margin of stranded beach ridges of aeolian calcarenite in South Australia from Blackburn, Bond and Clarke (1965) (dot and dash line) and the distribution of major areas of Diapur Sandstone, partly from Blackburn, Bond and Clarke (1967), shown by crosses. The only extensive ranges of pre-Cainozoic rocks in the whole area are the Mount Lofty and Grampians Ranges.

This leaves a dry area in and around the Ninety Mile Plain which becomes wetter towards the coast, but even there mean annual rainfall falls as low as 430 mm. This may prevent present day plant migration to and from south-western Victoria. In considering this dry coastal area as a possible past migration route it is relevant that the whole area south-east of the most inland stranded beach ridge of aeolian calcarenite (Fig. 1) is a lowland; pre-Cainozoic rocks are very rare and scattered and never form extensive ranges (Blackburn, Bond & Clarke 1965). Soils are predom-

inantly various infertile coastal sands, shallow sandy soils on limestones, and badly drained areas of clayey and peaty soils (Northcote 1960). Fertile, well-drained medium and heavy-textured soils are very rare.

Off the present South Australian coast, Pleistocene low sea-levels more than 49 m below present are definitely known (Sprigg 1965), while world-wide eustatic sea-level changes are thought to have produced a level about 120 m below present in the Last Glacial (Jelgersma 1966). On both the coastal lowland produced by such emer-

gence, and the coastal lowland present today, aeolian calcarenite is an important component (Sprigg 1952). It seems likely that aeolian calcarenite in the past was associated with a suite of soils similar to that now present, so that soils and topography on the Glacial lowland were probably similar to those of the present coastal area.

The disjunct eucalypts involved can be considered in four groups depending on which soils seem most likely to provide migration routes for them. Many of them occur on a wide range of other soils as well.

SPECIES KNOWN FROM SILICEOUS SANDS

All these species (Table 1) are common in coastal and sub-coastal areas on siliceous sands, in the case of *E. ovata* (Fig. 2) usually on peaty horizons over sand around swamp margins. All occur in the south-east of South Australia, and to provide a past migration corridor to the Mount Lofty Ranges, all that is required is an increase in effective rainfall with the sea at its present level.

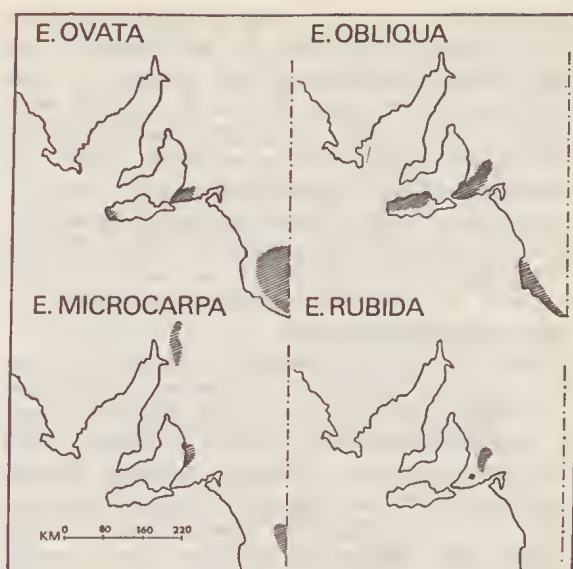


FIG. 2.—Distribution of four species of *Eucalyptus* in South Australia from Boomsma (1972).

TABLE 1

DISTRIBUTION AND HABITAT DATA FOR WESTERN VICTORIAN *Eucalyptus* SPECIES WITH DISJUNCT OCCURRENCES IN SOUTH AUSTRALIA, AFTER BOOMSMA (1972)

Approximate lower rainfall limit in South Australia (as mean annual rainfall in mm)		Occurrence in South Australia					References*
		Lower south-east	Upper south-east	Mount Lofty Ranges	Flinders Ranges	Kangaroo Island	
Species known from Siliceous Sands							
<i>E. baxteri</i>	460	X	X	X		X	Litchfield (1956)
<i>E. fasciculosa</i>	460	X	X	X		X	White (1970)
<i>E. obliqua</i>	610	X		X		X	
<i>E. ovata</i>	610	X		X		X	
<i>E. viminalis</i> complex	460	X	X	X		X	Litchfield (1956)
Species known from Aeolian Calcarenite							
<i>E. leucoxydon</i>	460	X	X	X	X	X	Litchfield (1956)
Species known from Medium and Heavy-textured Soils							
<i>E. microcarpa</i>	480		X	X	X		
Species known from Ranges of pre-Cainozoic Rock							
<i>E. goniocalyx</i>	580			X	X		
<i>E. macrorhyncha</i>	610				X		
<i>E. rubida</i>	760			X			

* In addition to Boomsma (1972)

Alternatively a Glacial drop in sea-level would expose country south-east of the present coast which would probably be wet enough to allow continuous distribution if rainfall regimes were the same as at present (see also Parsons 1969). This assumes that suitable soils were present on the Glacial coastal lowland, which seems likely.

Another disjunct species in this category for which similar explanations could apply is *Banksia marginata* (Boomsma 1972), as well, probably, as other sclerophyllous species with similar climatic and edaphic ranges.

Western Victorian species in this 'coastal-siliceous' category include *E. kitsoniana* which does not reach South Australia, and *E. vitrea** and *E. pauciflora* (as well as *Acacia mearnsii*) which reach the south-east of South Australia, but do not occur anywhere else in the state (Boomsma 1972). The reasons for these restricted distributions are enigmatic; perhaps these species reached western Victoria at a time when migration routes to the Mount Lofty Ranges were no longer available.

SPECIES KNOWN FROM AEOLIAN CALCARENITE

The one species in this group, *E. leucoxydon*, is rare on siliceous sands, but occurs on shallow soils on Pleistocene aeolian calcarenite, for example at Southend in South Australia (Fig. 1). The distribution of such soils (Northcote 1960) could easily provide a coastal migration corridor, under the same conditions as those specified for the previous group (some of which also occur on aeolian calcarenite).

SPECIES KNOWN FROM MEDIUM AND HEAVY-TEXTURED SOILS

E. microcarpa (Fig. 2) appears closely restricted to relatively fertile, well-drained medium and heavy-textured soils, and in keeping with this is absent from the south-east extremity of South Australia and all of the coast from there to the mouth of the Murray River. As soils near the present coast and possibly also of the Last Glacial coastal lowland seem unlikely migration routes, an alternative route may be necessary.

A more direct route linking the present occurrences near Bordertown in the upper south-east of South Australia with those near Adelaide would be along a straight line linking these two places, but this seems to be at least partly closed by sandy infertile soils in the Ninety Mile Plain.

* The type of *E. vitrea* R. T. Baker is considered by others to be a hybrid; if so the name could not be applied to this species (see Pryor, L. D. and Johnson, L. A. S., 1971. *A classification of the eucalypts*. Australian National University, Canberra).

The present occurrences near Bordertown are on cracking clay soils thought to indicate a former location of alluvial tracts on the Murray Basin plain (Blackburn 1962a). Extensive areas of deep heavy clays are known beneath the present land surface inland from the inland margin of aeolian calcarenite in the Ninety Mile Plain (Fig. 1) and these areas may also be related to former alluvial tracts on the Murray Basin plain (Litchfield 1956). It would be most interesting to know the former extent of surface clay in this area to see if it could have provided a suitable migration route for *E. microcarpa*.

Two species showing disjunctions according to Boomsma (1972), and which are possibly in this group, are *E. odorata* and *E. porosa*. These are omitted here, as difficulty in separating them means that their edaphic ranges are badly known and as Boomsma's (1972) maps do not appear to include all the records of them by Litchfield (1956). Taken together, these two closely related species may extend almost continuously from Bordertown to the Mount Lofty Ranges through the Ninety Mile Plain (Boomsma 1972, Litchfield 1956).

SPECIES KNOWN FROM RANGES OF PRE-CAINOZOIC ROCK:

E. goniocalyx is fairly closely restricted to slopes and foothills of Flinders, Mount Lofty and Great Dividing Ranges, usually on shallow, rocky or gravelly soils. Of the coastal records in Hall, Johnston and Chippendale (1970), some are on hillslopes of pre-Cainozoic rocks (e.g. near Melbourne) and others are likely to be errors (see Boomsma 1972, Parsons & Kirkpatrick 1972). As *E. goniocalyx* has not been recorded from coastal sands or any other coastal or near-coastal lowland soils in areas where climate is suitable for it, it is hard to envisage a continuous migration route near to the present coast or seaward from it in times of low sea level. The species is unknown from inland plains, so these are also unlikely migration routes. The most plausible migration route on pre-Cainozoic rocks would appear to be along the granite of the Padthaway Ridge in the Ninety Mile Plain area (Parkin 1969) at some stage in the Cainozoic. Although granite outcrops are very small and very scattered at present (Blackburn, Bond & Clarke 1965), they could have been more or less continuous from Pliocene to early Pleistocene times until much of the Ridge was probably submerged later in the Pleistocene (J. B. Firman pers. comm.). To provide a more recent continuous migration route on ranges of pre-Cainozoic rocks, species would have to migrate north up the Great Dividing

Range to Queensland and then follow the Gray and Barrier Ranges down to the Flinders Ranges.

However, there is an interesting exception to the general occurrence of *E. goniocalyx* on soils on pre-Cainozoic rocks. At its western limit in Victoria (Blackburn 1963) the species extends beyond ranges of such rocks, but only onto ridges of Diapur Sandstone (Blackburn pers. comm.), which is thought to be of Pliocene age (Brown, Campbell & Crook 1968). Soils on these ridges resemble those carrying *E. goniocalyx* on ranges of pre-Cainozoic rocks in their acidic topsoils; in the rocky, gravelly character imparted by their ironstone gravel and sandstone; and in their elevated position above the surrounding plains.

These ridges of Diapur Sandstone (equivalent to Parilla Sand) are thought to represent beach dunes stranded during the Pliocene retreat of the sea (Brown, Campbell & Crook 1968). To the west, very similar sandstone interpreted as equivalent to Diapur Sandstone occurs in the Marmon-Jabuk Range (Fig. 1) where it is buried by later sediments (Jessup & Wright 1971). Although this range is not at present continuous with the areas of Diapur Sandstone in Victoria, there is some Diapur Sandstone in the intervening area north of Bordertown (Blackburn 1962). If ridges of the sandstone do represent coastlines of the former Murravian Gulf (Jessup & Wright 1971), it is possible that they were formerly more or less continuous from near the Grampians almost to the Mount Lofty Ranges, so that they may constitute a possible migration route for *E. goniocalyx*. If such migration did occur, this would certainly imply a previous climate of higher effective rainfall than at present.

E. macrorhyncha has a very similar edaphic range to *E. goniocalyx* (with which it often cohabits), being both fairly closely restricted to pre-Cainozoic rocks, and absent from coastal lowlands or inland plains. Although it is not known from soils on Diapur Sandstone, it is known from very similar ironstone-rich soils on Tertiary deposits, as in the Brisbane Ranges near Melbourne. If a relatively continuous migration route has to be chosen on the basis of its present day ecological tolerances, again ridges of Diapur Sandstone may be more likely than the other routes available.

E. rubida (Fig. 2) is ecologically similar to the previous two species, but with a wetter lower rainfall limit (Table 1). Although often found on deeper soils than are *E. goniocalyx* and *E. macrorhyncha*, it is again absent from coastal lowlands and inland plains. Like *E. macrorhyncha* it appears to reach its western limit in Victoria in the Grampians area. It is not known from soils

on Diapur Sandstone or from similar soils and may more strongly suggest past migration on soils on pre-Cainozoic rocks like those of the Padthaway Ridge than the other species. In any case, past migration to the Mount Lofty ranges implies a previous effective rainfall higher than that necessary for migration of any other species considered (Table 1). Also, *E. rubida* extends to colder sites in the eastern states than *E. goniocalyx* and *E. macrorhyncha*, but whether this is significant for any past migrations is not known.

It is also of interest that many of the associates of *E. goniocalyx*, *E. macrorhyncha* and *E. rubida* on pre-Cainozoic ranges in Victoria, such as *E. dives*, *E. polyanthemus*, *E. radiata* and *E. sideroxylon* do not occur in South Australia. The reasons why *E. rubida*, for example, should occur in the Mount Lofty Ranges, but not these other species, are completely obscure.

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Th-230/U-234 GEOCHRONOLOGY OF MARINE SHELLS FROM NEAR SALE, E. VICTORIA, AUSTRALIA

By JAMES C. SCHORNICK, Jr.*

(Communicated by E. D. Gill)

ABSTRACT: Shells from a Quaternary marine bed in Gippsland, Australia, gave a date of 28,800 y BP by ^{14}C , but an average of 101,000 y by U/Th dating.

INTRODUCTION

This report represents the results of U/Th analysis on eight samples of marine shells from west of Lake Melanyara, Sale, E. Victoria, Australia. The samples were collected from the floor of a deep channel north of a drain along a road 1 mile ENE. of Sale by Edmund D. Gill of the National Museum of Victoria. Selection of samples to be analysed and preliminary treatment to remove matrix and other extraneous material was performed by Mr. Gill.

PROCEDURE

In our laboratory, triplicate samples were weighed to the nearest mg and dissolved in 2N HNO_3 . To the solution were added a few drops of perchloric acid, 14 mg of Fe (as $\text{Fe}(\text{NO}_3)_3$) to be used as a carrier, and to two of the samples a known amount of Th-228 and U-232 to be used as yield tracers. This was followed by evaporation to dryness to destroy any organic matter and to insure equilibrium between sample and tracer isotopes. The sample was then dissolved in HCl and precipitated with NH_4OH after which the precipitate was separated from the supernatant liquid by centrifuging. After washing the sample with distilled water and centrifuging again, the precipitate was dissolved in 8N HCl and equilibrated with isopropyl ether to remove the iron. The aqueous solution was then passed through an anion exchange column to effect separation of the uranium from the thorium. Each fraction was then passed through another anion column in 8N HNO_3 for further purification. The samples were mounted on stainless steel planchets by electrodeposition.

The samples were counted by means of alpha spectroscopy in an alpha pulse height analyser

system. With this system it is possible to distinguish between each of the three isotopes on each planchet (U-232, U-234, U-238 and Th-228, Th-230, Th-232). The raw data was fed into a computer where corrections for background and contribution of one peak to another were made. The final output listed the concentrations of uranium and thorium, activity ratios of the various isotopes, and the age of each sample.

RESULTS

We feel that the analytical results were extremely good and that the errors are probably conservative.

The data in Table 1 represent the average of the two spiked duplicates. Errors were computed on the basis of counting statistics only. Errors for the calculated ages are the same percentage as for the corresponding Th-230/U-234 ratio. Sample names were supplied by Dr. Norman Weisbord of the FSU Dept. of Geology. The numbering system is the same as supplied by Mr. Gill.

The uranium concentrations for the oyster shells are quite consistent and fall within the range normally exhibited by corals, i.e., 1-3 ppm. The clam shells, however, exhibited unusually high concentrations of uranium indicating possible post-depositional uptake of uranium. With the exception of AS-4 all samples showed a U-234/U-238 ratio much higher than the expected sea water value of 1.15. Although high, the ratios are generally quite uniform. These ratios indicate possible preferential uptake of U-234 over U-238.

Thorium concentrations are 0.5 ppm or less indicating little or no post-depositional uptake of thorium. Uptake of thorium, especially Th-230 would produce anomalously high ages.

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TABLE 1
AUSTRALIAN CARBONATE DATA

SAMPLE	U PPM	Th PPM	$\frac{U-234}{U-238}$	$\frac{U-234}{DPHFG}$	Th-230 DPHFG	$\frac{Th-230}{U-234}$	$\frac{Th-232}{U-234}$	AGE
AS-1 OYSTER	1.87 ± 0.07	0.05 ± 0.01	1.25 ± 0.03	103.0 ± 3	53.3 ± 3	0.52 ± 0.03	0.008	77,000
AS-2 OYSTER	0.63 ± 0.04	0.01 ± 0.02	1.20 ± 0.09	33.6 ± 2	21.2 ± 2	0.63 ± 0.06	0.006	104,000
AS-3 OYSTER	2.30 ± 0.09	0.33 ± 0.04	1.24 ± 0.03	126.0 ± 4	75.3 ± 3	0.60 ± 0.03	0.039	95,000
AS-4 OYSTER	0.30 ± 0.03	0.19 ± 0.06	1.13 ± 0.04	14.9 ± 2	9.75 ± 1	0.65 ± 0.10	0.182	112,000
AS-5 OYSTER	1.20 ± 0.07	0.29 ± 0.03	1.22 ± 0.06	65.1 ± 3	40.4 ± 2	0.62 ± 0.04	0.067	101,000
AS-6 CLAM <u>Neotrogonia</u> <u>margaritacea</u>	7.61 ± 0.30	0.34 ± 0.06	1.29 ± 0.03	436.0 ± 15	309.0 ± 10	0.71 ± 0.03	0.012	125,000
AS-7 CLAM <u>Anadara</u> <u>trapezia</u>	9.73 ± 0.50	0.16 ± 0.09	1.37 ± 0.03	591.0 ± 10	379.0 ± 65	0.64 ± 0.11	0.004	105,000
AS-8 CLAM <u>Anadara</u> <u>trapezia</u>	20.50 ± 2.00	0.55 ± 0.06	1.27 ± 0.02	1155.0 ± 100	669.0 ± 10	0.58 ± 0.05	0.007	90,000
Average Age								101,000

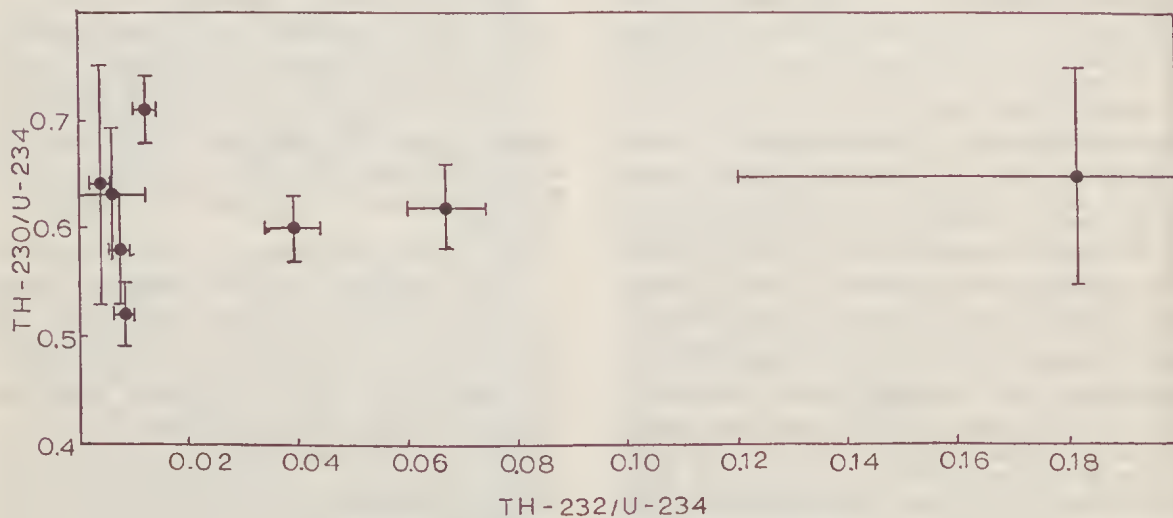


FIG. 1—Plot of Th-230/U-234 vx. Th-232/U-234.

The consistency of the Th-230/U-234 ratio, which is used to calculate the ages of the samples, is quite encouraging especially when dealing with a variety of shells. Calculated ages range from 77,000 years to 125,000 years with an average age of 101,000 years. The age is considerably greater than the reported ^{14}C age of 28,800 years, but the overall consistency of our data gives support to its validity.

In order to check on possible thorium contamination we applied the isochron method as described by Osmond, Tanner & May (1970). Fig. 1 is a plot of Th-230/U-234 vx. Th-232/U-234. With all of the Th-234/U234 values except one less than 0.07 and the Th-230/U-234 values fairly consistent, any isochron through these

points gives only a slightly lower age than the average age.

We conclude, therefore, that our age of 101,000 years is a reasonable value. The consistency of the data seems to rule out any thorium contamination and if any uranium was added to the system it was done soon after deposition, thus having little or no effect on the analysis. If uranium were added to the system more recently, the effect would be to yield apparent ages lower than the true ages.

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OPISTHOBRANCH MOLLUSCS FROM THE AUSTRALIAN SUB-ANTARCTIC TERRITORIES OF MACQUARIE AND HEARD ISLANDS

By ROBERT BURN*

ABSTRACT: Two species of opisthobranch molluscs are reported from Australian Sub-Antarctic territories. *Archidoris kerguelensis* Bergh 1884 occurs at Macquarie Island and Heard Island. *Trinchesia maquariensis* sp. nov. is described from Macquarie Island.

INTRODUCTION

Dell's (1964) lists of marine molluscs from Macquarie and Heard Islands include no opisthobranchs. Since then, one species has been reported from Macquarie Island (Merilees & Burn 1969). Other material was found in the collections of the National Museum of Victoria (NMV in text) and some additional specimens were presented to the Museum by Miss Isobel Bennett of Sydney and Mr. R. D. Simpson of Adelaide.

SYSTEMATIC DESCRIPTIONS

Family DORIDIDAE

Archidoris Bergh 1878

Archidoris kerguelensis Bergh 1884
(Fig. 1-7)

Archidoris kerguelensis Bergh 1884, p. 85, Pl. 1, fig. 1-12; Merilees & Burn 1969, p. 137.

Non *Archidoris kerguelensis* Bergh 1894, p. 159.

MATERIAL: NMV F17508, Heard Island, 4 specimens washed up on beach after storm, below camp at Atlas Cove, collected by Young and Gibbney, 16 August 1950; NMV F26579, Macquarie Island, 1 specimen from rock pool at low tide, Garden Cove, Buckles Bay, collected by W. Merilees, 16 June 1967; NMV F27408, Macquarie Island, 1 specimen from rock pool at low tide, Garden Cove, Buckles Bay, collected by Isobel Bennett, 23 March 1968.

DESCRIPTION: The larger preserved Macquarie Island specimen (F26579) measures 28 mm in length, 16 mm in breadth and 10 mm in height. The best preserved Heard Island specimen (Fig. 2) measures 30 mm in length, 18 mm in breadth, 12 mm in height, with the additional measurements of sole length 25 mm and breadth 11 mm, hyponotum breadth 3 mm, rhinophores 6 mm from anterior edge of notum, branchiae 3 mm from posterior edge, and branchial cavity 9 mm in transverse diameter. The largest but severely contracted Heard Island specimen is 48 mm in length and 28 mm in breadth.

Colour slides of the living Macquarie Island specimens, from which Fig. 1 was drawn, show them to

have pale yellow bodies, orange rhinophores and cream gills. Preserved Heard Island specimens are yellowish-orange with orange sole.

The moderately convex notum is covered with large hemispherical papillae, 1 mm diameter, surrounded by small cylindrical papillae generally 0.5 mm diameter and less. There are more large papillae in the median area than marginally. The patterning is less regular in the Heard Island specimens (Fig. 7a) than in those from Macquarie Island (Fig. 7b), with fewer but bigger, small or secondary papillae in the former specimens. Spicules project from some of the smaller papillae. The rhinophoral and branchial cavities have in some specimens small and large papillae along the edges, but in others these cavities are smooth-margined or irregularly formed. The branchial cavity is transversely oval, very shallow and filled by eight bipinnate gills. The gills are best described as contractile rather than retractile, as the cavity is incapable of closure. The fluted anal papilla stands between the rear pair of gills. The rhinophores have 11-14 lamellae. The foot is entire in front (Fig. 3), the head is large and rounded, with indistinctly grooved oral lappets each side.

The labium is thin and smooth. In the larger Macquarie Island specimen, the very pale yellow radula is 4 mm long by 2.5 mm wide with 22 rows of 29.0.29 teeth. The largest Heard Island specimen has a 10 x 6 mm brown radula with 24 rows of 36.0.36 teeth. In the smallest Heard Island specimen, 25 mm in length, the radula is 6.5 x 3.5 mm with 22 rows of 30.0.30 teeth. The teeth in the Macquarie Island specimen (Fig. 5) increase at first slowly (1-7), then sharply (8-13), thereafter decreasing a little (14-27) with short slender marginals. The Heard Island specimens (Fig. 6) show a gradual increase in size in the first 10 teeth, and a sharp decrease in the marginal five or six teeth. All teeth are uniformly hook-shaped.

The anterior genital mass in the largest Heard Island specimen is ovate in shape and measures 22 x 17 mm (Fig. 4). The long fusiform ampulla (b) is white and lies on both anterior and posterior faces of the mass. At the distal end it branches to the wide male (vd) and female (i) ducts. The first part

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of the 35 mm long and 1 mm diameter muscular vas deferens is folded two or three times, thereafter running with a few bends to the dilated penial sheath, into the fundus of which projects the 1 mm long conical penial papilla (p). The vagina, 1 mm in diameter, is short and folded once at its inner end (v); its opening into the genital atrium lies beside the mouth of the penial sheath. The thin-walled spherical spermatheca (st) and curved muscular spermatocyst (sc) are attached vaginally; they lie deeply embedded in the yellow mucous gland (m). The tapering insemination duct (i) is short and folded several times.

In the larger Macquarie Island specimen, the anterior genital mass is flatter and smaller, and the male and female ducts have precisely the same paths except that the spermatocyst lies against the vagina. The penial papilla is 0.3 mm long and wide.

REMARKS: The well-preserved Macquarie Island specimens are distinguished from the storm-tossed Heard Island specimens in several aspects. They are somewhat smaller than all but the smallest strongly contracted Heard Island specimen. The notal papillae are slightly smaller, and more regularly disposed, with clearly defined rings of secondary papillae around the primary papillae. The dimensions of the radula are considerably smaller than in the smallest Heard Island specimen, yet the numbers of rows and teeth per row are almost identical. The gradation of the teeth per radular half-row differs, with more teeth of the same size in the Heard Island specimens. More material from both localities would reduce any significance in these differences, and they are here regarded as intra-specific variants of one species.

The original specimen of *A. kerguelensis* Bergh 1884 was dredged from 25 fathoms off Royal Sound, Kerguelen Islands. It measured 45 mm in length, 18 mm in breadth and 12 mm in height, and was yellowish in colour with varying-sized papillae all over the notum and small papillae along the rims of the rhinophoral and branchial openings. The rhinophores had 30-40 lamellae; there were seven gills. The labium was soft and smooth, the radula had 27 rows of at most 40.0.40 teeth. The globular spermatheca and curved spermatocyst were attached close together to the top of vagina and insemination duct, the vas deferens was long, thick, non-prostatic, and terminated in a small conical penial papilla.

The Macquarie and Heard Island specimens appear to have larger notal papillae than Bergh specifies in his description, and at most half the number of rhinophoral lamellae. According to Mrs. Eveline Marcus (pers. comm.), Bergh sometimes counted the lamellae on both sides of the rhinophoral clavus, thus 15-20 is probably the correct count in the Kerguelen type and much closer to the count of 11-14 in the present specimens. The present radulae have fewer rows and fewer teeth per row, even though the largest Heard Island specimen is larger than the Kerguelen type. The attachment of the spermatheca and spermatocyst is vaginal in specimens from both islands, whereas Bergh with only one specimen at his disposal described the spermatocyst as attached to the base

of the insemination duct. Again, these differences appear to be intra-specific, thus insufficient to preclude identifying the Macquarie and Heard Island specimens with *Archidoris kerguelensis* Bergh from the Kerguelen Islands.

The relationship of the molluscan faunas of Macquarie and Heard Islands to each other and to that of the Kerguelen Islands has been discussed by Powell (1955, 1960) and Dell (1964). Both authors emphasize the strong endemism of the faunas and their link with the fauna of the Kerguelen Islands. Therefore, it is not surprising that *A. kerguelensis* occurs at all three places.

Archidoris Bergh 1878 is a genus of large to medium sized species. Besides *A. kerguelensis* described above, the following species were examined in the course of this research; the type species *A. tuberculata* (Cuvier 1804) from Salcombe, England, *A. montereyensis* (Cooper 1862) and *A. odhneri* (MacFarland 1966) from Friday Harbour, Washington, U.S.A., *A. wellingtonensis* (Abraham 1877) from New Zealand and Australia, and a new species from Sydney, New South Wales. Of these five species, *A. tuberculata*, *A. montereyensis* and the new species have notal ornamentation (Fig. 7c-e) similar to that of *A. kerguelensis* (Fig. 7a-b), namely large papillae set in a field of small papillae. Characteristics which separate these species from *A. kerguelensis* are: in *A. tuberculata*, an exceptionally long winding vas deferens and long tapering penial papilla; in *A. montereyensis*, a long winding vas deferens and long penial papilla; in the new Australian species, a shorter radula, shorter vas deferens and smaller penial papilla.

The other two species have a very different notal ornamentation from the species of the *A. tuberculata* group. Large and small irregular but low papillae occur in *A. odhneri* (Fig. 7f), and large regular hemispherical papillae in *A. wellingtonensis* (Fig. 7g). The male ducts too are very different, with a broad variable penial papilla, and a large sheath of fibrous tissue through which passes the outer part of the vas deferens. From its description and figure, the South African *A. scripta* Bergh 1907 belongs to this group, even though the notum is described as smooth.

Species of the antarctic genus *Austrodoris* Odhner 1926 are very similar to *A. kerguelensis* and the new Australian species in the length of the vas deferens and absence of a prostatic section. However, *Austrodoris* has a tough leathery sheath enclosing the vas deferens for its whole length and is devoid of a penial papilla.

The following list gives reputed species of *Archidoris*, for which details of the genital organs have not been described:

- africana* Eliot 1903, East Africa
- australis* Bergh 1884, Kerguelen Islands
- capensis* Bergh 1907, South Africa
- fulva* Eliot 1907, Australia
- granosa* Bergh 1907, South Africa
- kurana* Bergh 1905, Indonesia
- minor* Eliot 1903, East Africa
- nanula* Bergh 1904, New Zealand
- violacea* Bergh 1904, New Zealand

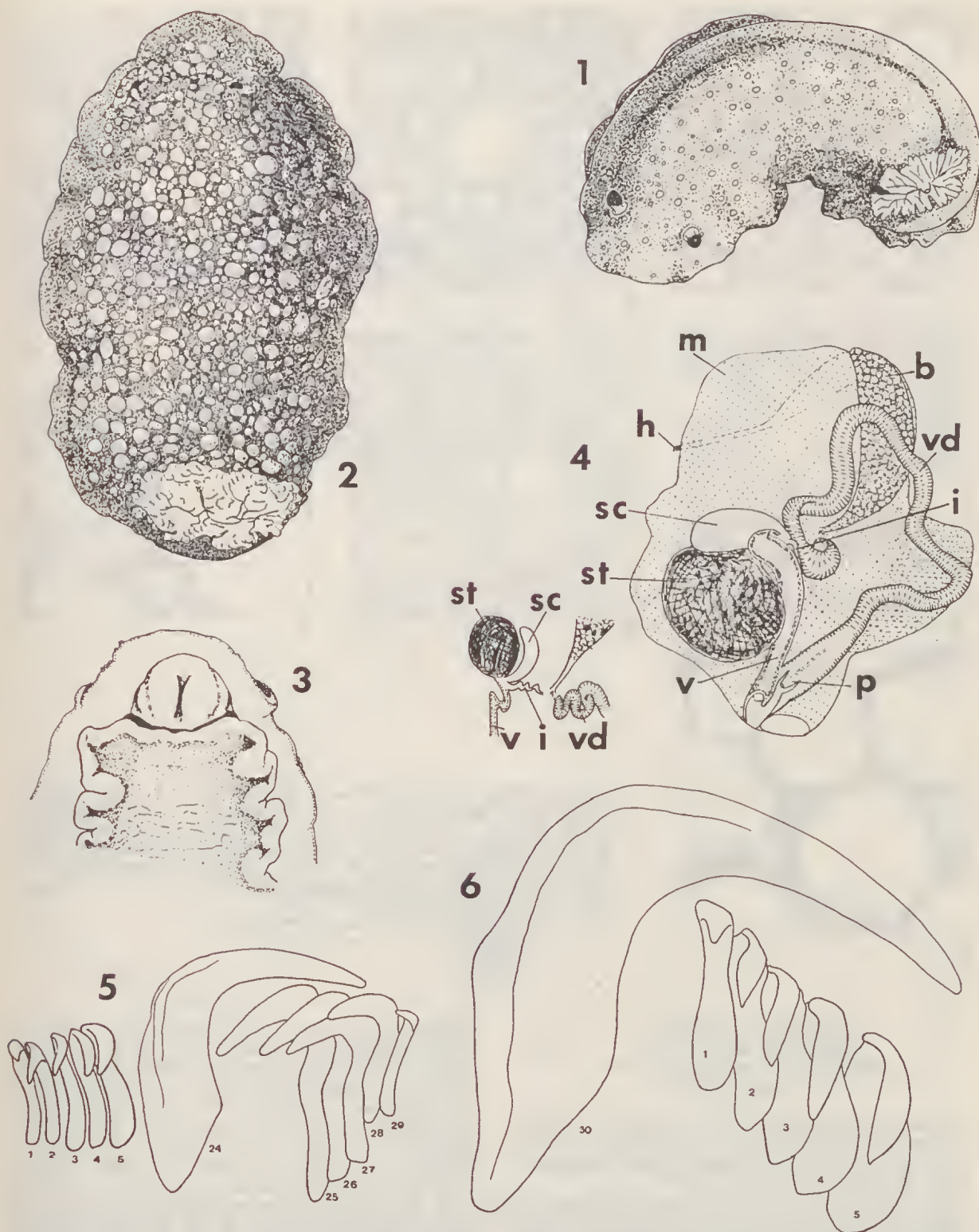


FIG. 1-6—*Archidoris kerguelensis* Bergh. 1—Larger Macquarie Island specimen, drawn from a colour slide. 2—Heard Island specimen, length 30 mm. 3—Ventral aspect of anterior of Heard Island specimen. 4—Reproductive organs. 5—Radular teeth from Macquarie Island specimen. 6—Radular teeth from Heard Island specimen. Abbreviations: b—ampulla, h—hermaphrodite duct, i—insemination duct, m—mucous gland, p—penial papilla, sc—spermatocyst, sp—spermatheca, v—vagina, vd—vas deferens.

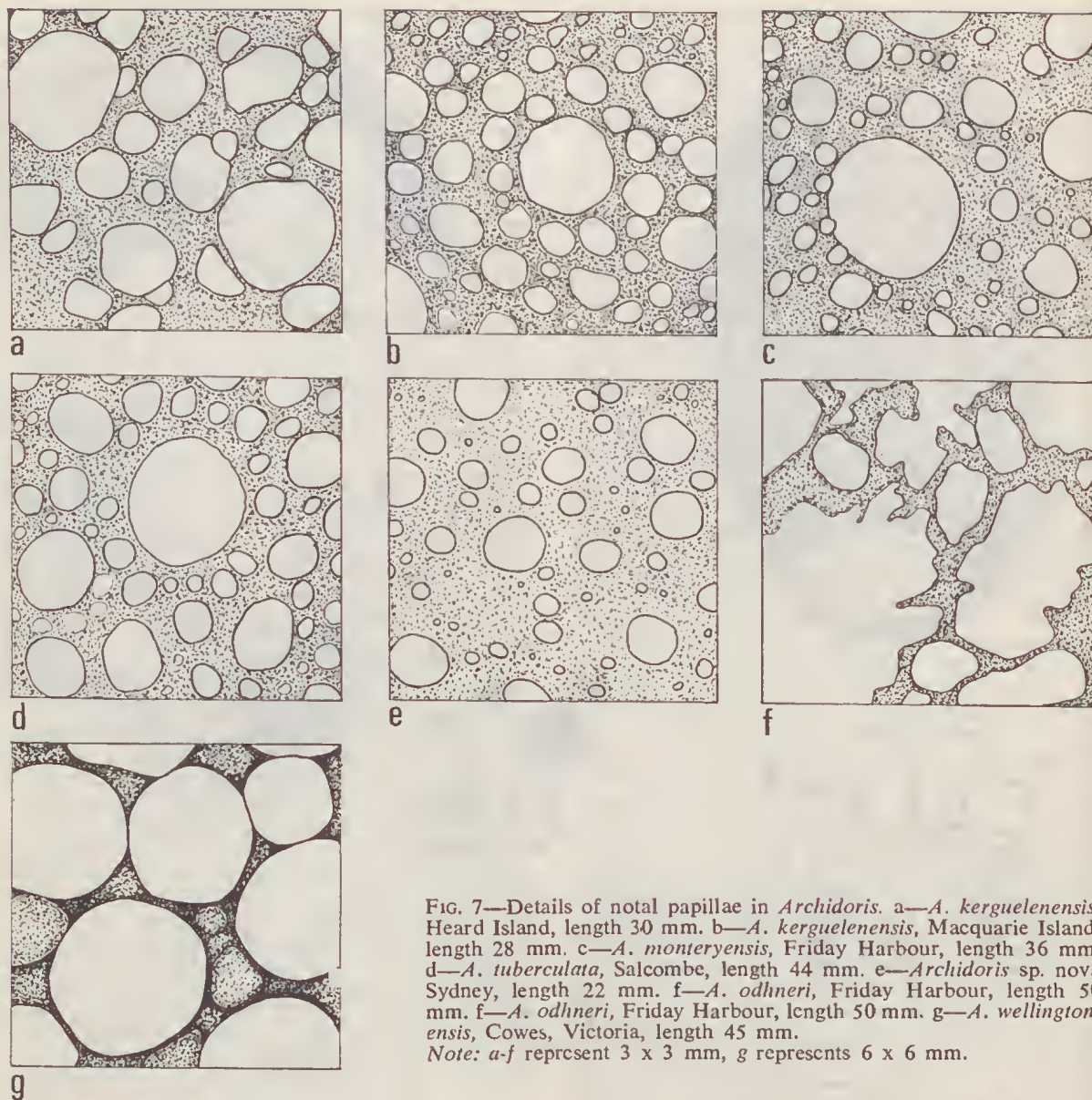


FIG. 7—Details of notal papillae in *Archidoris*. a—*A. kerguelensis*, Heard Island, length 30 mm. b—*A. kerguelensis*, Macquarie Island, length 28 mm. c—*A. montereyensis*, Friday Harbour, length 36 mm. d—*A. tuberculata*, Salcombe, length 44 mm. e—*Archidoris* sp. nov., Sydney, length 22 mm. f—*A. odhneri*, Friday Harbour, length 50 mm. g—*A. wellingtonensis*, Cowes, Victoria, length 45 mm.

Note: a-f represent 3 x 3 mm, g represents 6 x 6 mm.

Family CUTHONIDAE
Trinchesia Ihering 1879
Trinchesia macquariensis sp. nov.
 (Fig. 8-12)

MATERIAL: Holotype, NMV F27406, from red alga *Plocamium hookeri* Harvey, 60 m offshore at 5 m depth in Buckles Bay, Macquarie Island, collected by R. D. Simpson, 19 December 1968.

Paratype, NMV F27407, from small algae and encrusting corallines in rock pool at Garden Cove, Buckles Bay, Macquarie Island, collected by Isobel Bennett, 23 March 1968.

DESCRIPTION: Alive, the holotype was 5 mm in length and pink in colour; preserved it is nearly 4 mm long with rhinophores 1.6 mm long and cerata up to 2 mm long, and the colour is uniformly white. The preserved paratype is white, 5 mm long with rhinophores 1.7 mm and cerata up to 2.25 mm in length. The slender body is widest at the head and highest at the level of the anus in the cardiac region. The slender fusiform cerata stand in three rows of 1, 3, 3 in the anterior liver and five rows of 3, 2, 2, 2, 1 in the posterior liver of the holotype (Fig. 8); the paratype has four rows of 2, 3, 4, 5 cerata in the anterior liver and five rows of 3, 3, 2, 2, 1 cerata

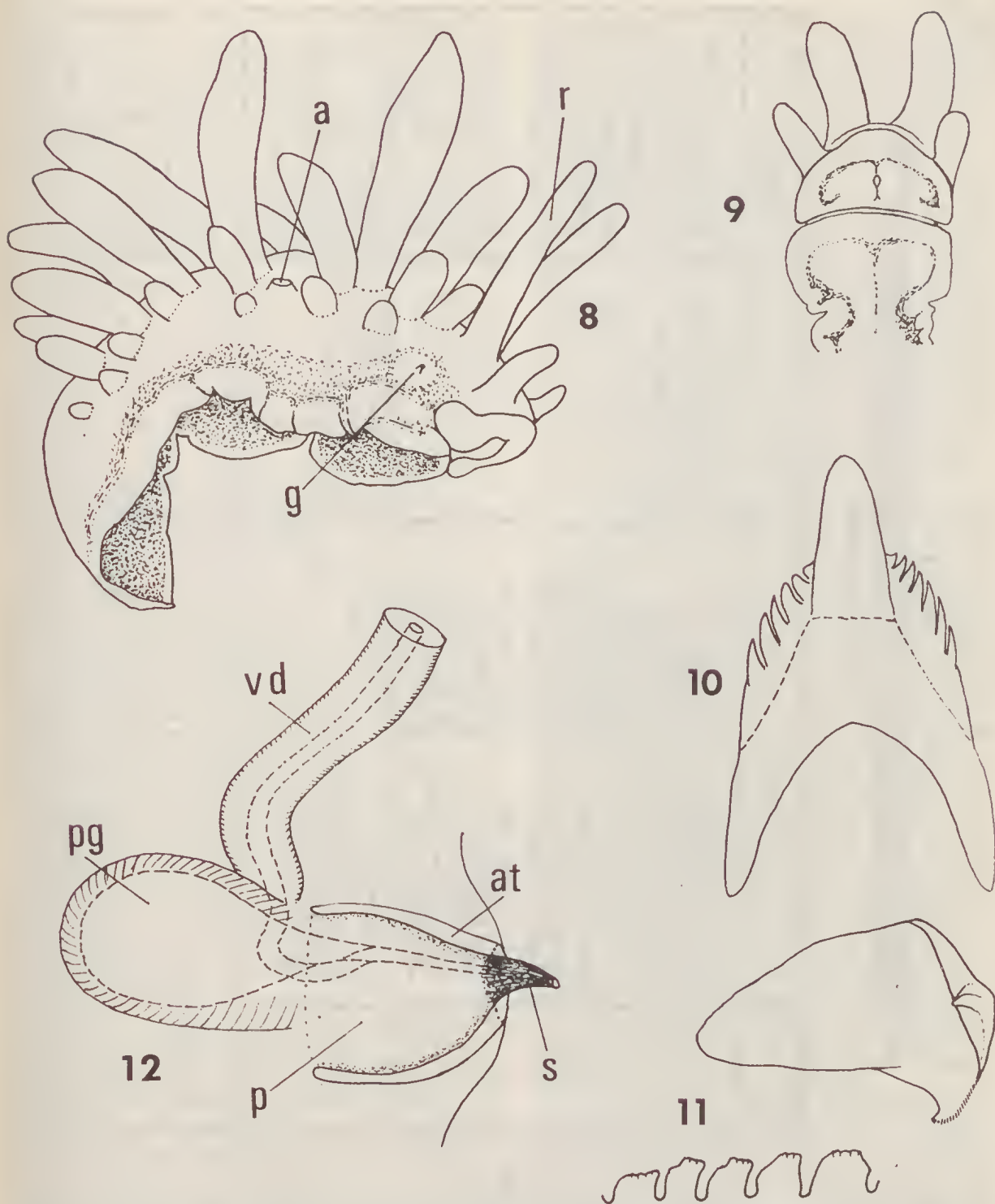


FIG. 8—12—*Trinchesia macquariensis* sp. nov. 8—Preserved holotype from right side. 9—Ventral aspect of head of holotype. 10—Radular tooth. 11—Jaw and details of masticatory border. 12—Male copulatory organs. Abbreviations: a—anus, at—atrium, g—genital aperture, p—penis, pg—penial gland, r—rhinophores, s—stylet, vd—vas deferens.

in the posterior liver. The genital aperture opens below the first, or first and second rows of the right anterior liver, the anus stands before the space between the two larger cerata of the first row of the right posterior liver. The anterior foot corners (Fig. 9) are rounded, the tentacles and rhinophores are slender and smooth, and the mouth is deeply recessed.

The yellowish jaws are 1.1 mm long in the paratype, clongate in shape with 31 coarse denticles on the border (Fig. 11). The radula comprises 20 hyaline teeth up to 0.2 mm long in a single series, with prominent cusp and six or seven smaller lateral denticles each side (Fig. 10).

A colourless tubular stylet projects from the genital aperture of the holotype. In the paratype (Fig. 12), the 0.4 mm long by 0.26 mm diameter penis (p) bears a hollow cuticular stylet (s) 0.14 mm long at its tip; the penial gland (pg) which opens into the penis is 0.35 mm long and 0.24 mm in diameter; and the thick vas deferens (vd) has no prostatic section.

REMARKS: The presence of a cuticular penial stylet distinguishes *T. macquariensis* from all Antarctic and Sub-Antarctic cuthonid species described to date, with the exception of *T. valentini* (Eliot 1907) from the Falkland Islands. However, *T. valentini* is a larger species, 10 mm long preserved, with fewer cerata in rows of not more than two, a less prominent radular cusp and 7-9 more prominent lateral denticles, and in life a brownish body and cerata.

Geographically close species of *Trinchesia* from southern temperate waters of New Zealand, Australia and South Africa all differ from *T. macquariensis* in colour pattern, jaw and radular details, and in various aspects of the genital system (Morton & Miller 1968, Burn 1962, 1963, 1964, Macnae 1954).

The other species listed in Table 1 with penial stylet present, prostatic vas deferens absent are separated from *T. macquariensis* by colour and radular shape. *T. lagunae* (O'Donoghue 1926) (= *T. rutila* (MacFarland 1966)) has an orange-coloured V-shape on the head, orange-coloured rhinophores and ceratal tips, and brown digestive glands, plus a radular cusp not longer than the lateral denticles. *T. virens* (MacFarland 1966) has yellow ceratal tips and light green digestive glands, and the radular cusp not longer than the lateral denticles.

Edmunds (1964, 1968, 1969, 1970) and Edmunds and Kress (1970) have clearly demonstrated that the presence or absence of a penial stylet is of specific, rather than generic value in the Eolidacea. Application of this principle to the family Cuthonidae, where there is small morphological variation (Miller 1971), necessitates abandonment of the subfamilies Cuthoninae (without stylet) and Tergipedinae (with stylet) earlier proposed by the writer (Burn 1963, 1964).

This principle also allows the transfer to *Trinchesia* of those species previously assigned to *Cuthona* which have a penial gland, a condition contrary to that found in the type species of the latter genus, *C. nana* (Alder & Hancock 1842), (Odhner 1939, 1944). Table 1 lists, according to the available knowledge

of their reproductive systems, all the species that the writer regards as belonging to *Trinchesia*. It includes the '*Cuthona*' species with penial gland, plus the type species of the monotypic genera *Xenocratena* Odhner 1940, *Subcuthona* Baba 1949, *Narraeolida* Burn 1961, *Toorna* Burn 1964, and *Njurja* Marcus & Marcus (1960a), none of which can be maintained in an expanded genus that allows a shorter or longer radular cusp and armed or unarmed penis.

One might also ponder whether or not *Tenellia* Costa 1866, whose type species *T. adspersa* (Nordmann 1845) (= *T. pallida* (Alder & Hancock 1855)) (Marcus & Marcus 1955, 1960b) has a velum in place of cephalic tentacles, can be retained as a genus separate from *Trinchesia*, in view of their otherwise close similarity. The occurrence of a second species *T. fuscata* (Gould 1870), undoubtedly congeneric with the type of *Tenellia* but specifically distinct from it, suggests that this genus should be retained at least with subgeneric status. Also, *Tergipes* Cuvier 1805, in which the right liver is reduced to one branch with one ceras, is morphologically very similar to *Trinchesia*. They are probably congeneric, and if this is proved, *Tergipes* will have priority.

Three cuthonid genera with a penial gland and simple branches of the liver are distinct from the *Trinchesia*/*Tenellia*/*Tergipes* group. In *Catriona* Winckworth 1941 the pre-radula is retained, the radular teeth distinctively formed with minute accessory denticles between the larger denticles, and the masticatory borders of the jaws composed of bundles of bristles. In *Selva* Edmunds 1964 the anus is in the cleioproctic position. In *Phestilla* Bergh 1874 the cephalic tentacles are greatly reduced, the cerata stand upon raised flanges, and there are no cnidosacs. A penial gland attached to the base of the penis, non-prostatic vas deferens and unarmed penis are other characteristics of *Phestilla melanobranchia* Bergh 1874, the type of the genus (pers. obs.).

Genera with laterally multiplying branches of the liver are *Cuthonella* Bergh 1884, *Guyvalvoria* Vaysière 1906 and *Precuthona* Odhner 1929. The first two have the anus opening on the dorsal or median side of the cerata, *Cuthonella* with a slender penial gland attached by a narrow duct to the mid-length of the non-prostatic vas deferens, *Guyvalvoria* with the penial gland attached to the base of the penis and a prostatic vas deferens. In *Precuthona*, the anus is somewhat cleioproctic in that it occurs within the foremost liver branch of the posterior liver, the penial gland opens into the penis and the vas deferens is prostatic. These genera are very closely related to the *Trinchesia*/*Tenellia*/*Tergipes* group.

Genera without a penial gland are *Cuthona* Alder & Hancock 1855 and *Embletonia* Alder & Hancock 1851. Besides the type species *C. nana* (Alder & Hancock 1842), *Trinchesia sororum* Burn 1964 and *Catriona urquiza* Marcus 1965, both without penial gland, belong to *Cuthona*. *Embletoniella* Baba 1967 which has four apical twigs or nodes to each ceras, no cnidosacs, and a prostatic unarmed penis should be reduced to either a synonym or at most a subgenus of *Embletonia*.

The penial gland is not described for the genera *Indocratena* Odhner 1940, *Cratenopsis* Lemche 1935, *Ennoia* Bergh 1896, *Myja* Bergh 1896 and *Zatteria* Eliot 1902, all classified as Cuthonidae by their authors.

ACKNOWLEDGMENTS

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THE DISTRIBUTION OF *NOTHOFAGUS CUNNINGHAMII* RAINFOREST

By TRUDA M. HOWARD** and D. H. ASHTON*

ABSTRACT: In Victoria, *Nothofagus cunninghamii* is distributed in three main regions, the Central Highlands, Otway Ranges and Strzelecki-Wilsons Promontory area. In these regions it is found chiefly in gullies where annual rainfalls exceed 150 cm (60 in). On the basis of floristics, the *Nothofagus cunninghamii* and allied forests were divided into three associations which correspond to altitudinal zones 0-650 m (0-2000 ft), 650-1300 m, (2000-4000 ft) and over 1300 m (4000 ft). The associations correspond to the structural forms of tall closed forest, closed forest and low closed forest (Specht 1970) which correspond in turn to nanophyll mossy and fern forests, (Webb 1959, 1968); all these types were formerly called cool temperate rain forest (Wood & Williams 1960). The tall closed forest is rich in fern species and the low closed forest relatively rich in herb species. It is suggested that the forests may be expanding and that neither *Atherosperma moschatum* nor *Nothofagus cunninghamii* have fully exploited new niches due to difficulties of dispersal.

INTRODUCTION

Plant communities containing *Nothofagus cunninghamii* are distributed over much of the western half and north-eastern corner of Tasmania and in the southern central region of Victoria (Fig. 1). In both regions *Nothofagus* may occur either as a forest or scrub or as an understorey to various species of eucalypts, and extend from sea level to the sub-alpine regions. In Victoria it occurs chiefly along rivers and gullies and rarely on mountain sides and plateaux. In Tasmania, however, it may occur over a wide range of topographic situations.

ALTITUDINAL ZONATION

In Victoria *Nothofagus cunninghamii* is associated in forests with *Acacia melanoxylon*, up to 650 m (2000 ft), and with *Atherosperma moschatum* up to 1375 m (4200 ft). At higher altitudes it forms low forest with *Leptospermum grandifolium* up to its limit at 1570 m (4800 ft). Over the last 65 m (200 ft) of its range it may also be associated with *Podocarpus lawrencei*.

Nothofagus cunninghamii may form an understorey of variable density to *Eucalyptus viminalis* up to 650 m (2000 ft), to *E. regnans* from 195-1150 m (600-3500 ft), to *E. delegatensis* from 985-1470 m (3000-4500 ft), to *E. nitens* from

950-1250 m (2900-3800 ft) and to *E. pauciflora* from 1420-1570 m (4300-4800 ft).

In Fig. 2, the distribution of *Nothofagus cunninghamii* in Victoria on a 7½ minute grid is mapped. This shows the three general regions in which it is found: the Otway Ranges, the Central Highlands and South Gippsland-Wilsons Promontory. *Atherosperma moschatum* is more widespread to the E. and NE. of the state, occurs with *Nothofagus cunninghamii* in the central regions and is notably absent from the Otway Ranges. *Acacia melanoxylon* is widely distributed from E. to W. in southern Victoria, and *Leptospermum grandifolium* occurs in most gully areas of poor drainage above 1300 m (4000 ft), but is also found in such situations in some montane and lowland regions.

THE *Nothofagus cunninghamii* COMMUNITY

The floristics of representative mature *Nothofagus cunninghamii* communities (and those closely allied to them) were studied throughout their geographic and altitudinal range in Victoria. This range includes closed stands in which a mature eucalypt stratum is present or absent. The lists of species occurrence are given in Table 1.

There are few species of tree in any one stand. The closed forest consists of one to three species

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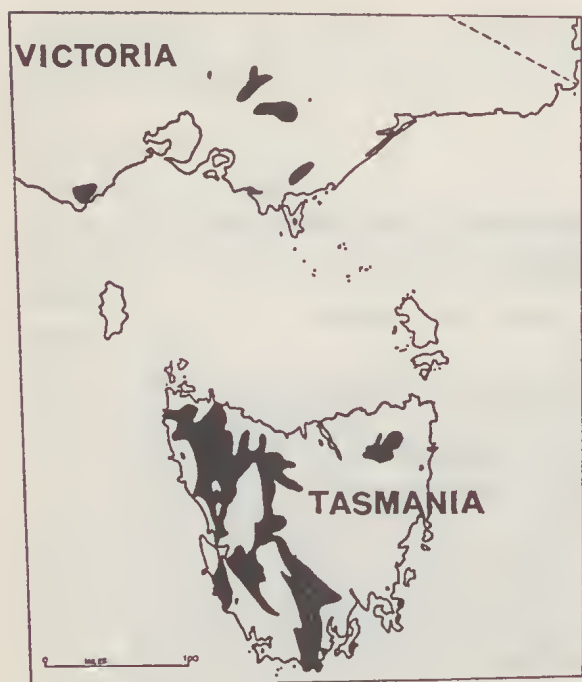


FIG. 1—The distribution of *Nothofagus cunninghamii* Oerst in South Eastern Australia.

of trees which range in height from about 42 m (130 ft) in the lowlands to 8 m (25 ft) at the highest altitudes. *Nothofagus cunninghamii* is dominant in most stands below 1300 m (4000 ft) and is co-dominant in those over this altitude. *Atherosperma moschatum* individuals rarely exceed 23 m (70 ft) in height, and this species is sub-

dominant to *Nothofagus cunninghamii* or *Acacia melanoxylon* (Petrie, Jarret & Patton 1929). In the absence of the latter two species, such as on the Errinundra Plateau (EI), *Atherosperma* reaches 33 m (100 ft) in height. The eucalypts, where they occur in association with *Nothofagus* below 1400 m (4300 ft), range in height from 33-82 m (100-250 ft) or more. Above this altitude they may reach only 13-16 m (40-50 ft) in height. A number of other tree and shrub species are present, but they are generally sparse and many are ecotonal in character and assume floristic importance only because many of the rain forest stands are so restricted in area. The species which are more characteristic of the closed forests are *Hedycaria angustifolia*, *Pittosporum bicolor* and *Coprosma nitida* and *Podocarpus lawrencei* at higher altitudes.

Lianes occur chiefly below 820 m (2500 ft) and are never abundant, *Clematis aristata* and *Parsonia brownii* being the most frequent.

Under the undisturbed canopy, herbs are generally sparse and include *Australina muelleri*, *Sambucus gaudichaudiana*, *Ucinia tenella*, *Luzula campestris*, *Libertia pulchella* and *Wittsteinia vaciniacea*. Where gaps occur in the canopy these species may be denser and associated with *Hydrocotyle javanica*, *Viola hederacea*, *Geranium 'pilosum'*, *Tetrarrhena juncea* and *Festuca dives*.

Ferns are conspicuous members of the forest and show a pronounced altitudinal zonation. Tree ferns are a characteristic feature of these forests up to 1400 m (4300 ft) *Dicksonia antarctica* is the commonest species throughout this range and is associated with *Cyathea australis* below 950 m

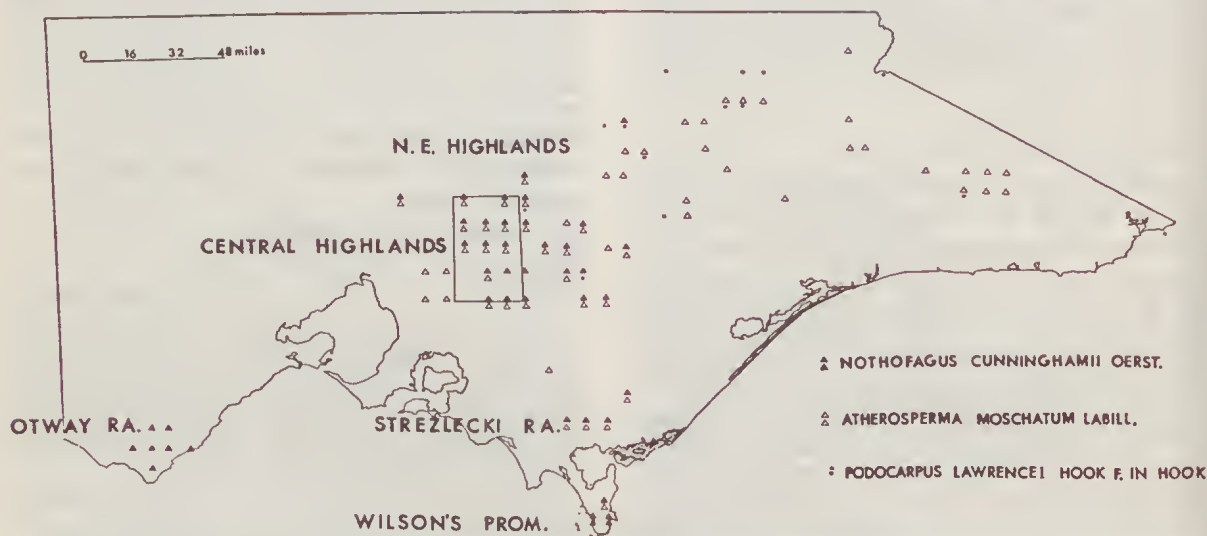


FIG. 2—The distribution of *Nothofagus cunninghamii* and *Atherosperma moschatum* in Victoria mapped on their occurrence in $7\frac{1}{2}$ minute grid squares.

(2900 ft). *Cyathea cunninghamii* and *C. marcescens* are rare and occur in Otway, Strzelecki and Wilsons Promontory forests below 490 m (1500 ft). Ground ferns such as *Polystichum proliferum* and *Blechnum procerum* also occur in adjacent eucalypt forests, and are much more abundant in the gullies where canopy openings are present. *Blechnum aggregatum*, *B. fluviatile*, *B. pattersonii* and *Asplenium bulbiferum* occur along stream banks, often in dense shade. At higher altitudes, greater than 1370 m (420 ft), *Blechnum penna-marina* is common.

The majority of epiphytic fern species occur below 820 m (2500 ft). The commonest species in the lowland forests are *Rumohra adiantiformis*, *Microsorium diversifolium*, *Grammitis billardieri*, *Asplenium bulbiferum* and the filmy ferns, *Mecodium australe*, *M. flabellatum*, *Hymenophyllum cupressiforme* and *Polyphlebium venosum*, all of which may also occur on rocks and logs. One filmy fern, *Hymenophyllum peltatum* occurs only at higher altitudes. Below 490 m (1500 ft) *Tmesipteris billardieri* is widespread although never abundant.

The epiphytic orchids *Corybas dilatatus* and *Sarcocochilus anstralis* also occur at lower altitudes. *Fieldia australis* occurs below 650 m (2000 ft) in the Strzelecki, Beenak and Wilsons Promontory forests as epiphytic espalier-form shrubs. Many tree and shrub species may establish as epiphytes on *Dicksonia antarctica* trunks below 980 m (3000 ft).

Bryophytes and lichens are very characteristic of these forests and increase in species and abundance with increasing altitude. At high altitudes they clothe tree trunks, logs, rocks and soil. At low altitudes they rarely occur on soil (except steep stream banks) but pendulous mosses commonly hang from the tree canopy in long strands. Dendroid mosses are common at the lower altitudes and do not extend beyond about 1150 m (3500 ft).

CLASSIFICATION OF *Nothofagus cunninghamii* AND ALLIED FORESTS IN VICTORIA

The forests described here have been classified broadly as temperate rainforest by Wood and Williams (1960) and have been segregated as the cool facies of the temperate type by Webb (1959). These forests were later classified by Webb (1968) on the basis of predominant leaf size and dominant trees, as nanophyll mossy forest. However, in Victoria, ferns are a very characteristic feature of the forests up to 1300 m (4000 ft) and it may be more appropriate to call these nanophyll fern forests. The forests have been further classified

according to dominant tree height and canopy cover, as suggested by Specht (1970).

Although, as a whole, *Nothofagus* closed forests present a uniform aspect, sufficient floristic and structural diversity was present to warrant a detailed analysis. Seventeen readily accessible mature stands (Nos. 1-17, Table 1) were studied, and their species composition assessed from the total number of species present in five random $2 \times \text{m}^2$ quadrats at each site. This combination of size and number of quadrats was chosen after initial work had been carried out at Mt. Donna Buang to determine the area which contained 85% of the species in the stand. Data on density, basal area and average height were collected also at each sample site.

The floristic data was analysed by a Similarity Analysis Program (Lance & Williams 1966) entitled CENTCLAS.

(a) FLORISTICS

The results of the similarity analysis were printed as two hierarchical diagrams (Fig. 3). The 'normal' analysis shows the grouping of sites in terms of their species similarity and the 'inverse' shows the grouping of the species in terms of their site similarities. A subjective decision was made about the number of groups in each analysis which might yield useful information, four (ABCD) in the 'normal' analysis where only 17 sites were involved, and a larger number, 9, (Z-R) in the 'inverse' analysis where 129 species were being analysed. The species components of each site group (A-D) were obtained by tabulating these groups against each of the species groups (Z-R). The percentage probability of a species occurring in a particular site group was then calculated as follows:

$$\frac{\text{No. of species/site coincidences realized}}{\text{Total no. of species/site coincidences possible}} \times 100$$

The values obtained for all species/site blocks were then ranked into four categories. Species occurring in more than 75% of sites in one site/species block were considered to have a high probability of occurrence at any site within this block, species occurring in 74-50% of sites to have an intermediate probability, and those in 49-25% to have a low probability of being found at any site in the site/species block. Species present in less than 24% of site/species blocks were considered unimportant in characterizing the site (A-D) groups.

Each of the nine species groups considered from the 'inverse' analysis remained separate on the basis of these calculations; however, in the case of the 'normal' analysis, the four groups originally considered (A-D), were reduced to three by the

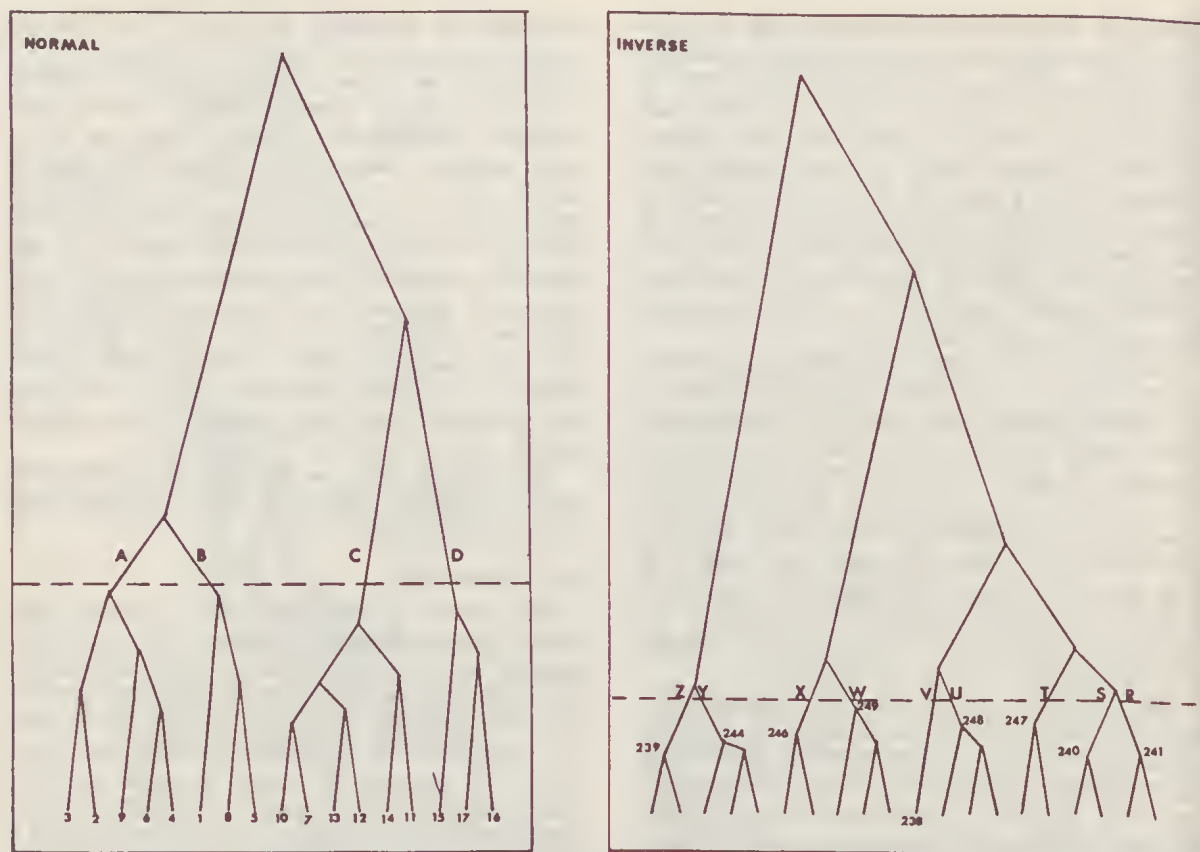


FIG. 3—Results of the Similarity Analysis 'CENTCLAS'. The normal analysis shows the hierarchy of groups into which sites were divided on the basis of their species composition. The inverse analysis shows the groups into which the species were divided on the basis of their site similarities. The broken lines across each level indicate the categories that were considered to be ecologically meaningful. The letters A-D and Z-R respectively indicate the site and species groups which were plotted against each other. The numbers indicate either sites (1-17 as in Table 1) or species groups, the subdivision of which is not shown in the inverse hierarchy.

fusion of A & B, there being no difference in species probability between these latter groups. The groups A-B, C and D remained separate from each other and can be interpreted as reflecting the effect of changes in altitude on the *Nothofagus* community. Sites within A & B all occur below 650 m (2000 ft) (tall closed forest), in C all occur between 650-1300 m (2-4000 ft) (closed forest) and all sites in D occur over 1300 m (4000 ft) (low closed forest). A summary of species probability of occurrence in each of these altitudinal associations is shown in Table 2. Their geographical distribution is shown in Fig. 4.

The major differences between the stands over 1300 m (4000 ft) and those below are the high (over 75%) probability of occurrence of *Leptospermum grandifolium* and *Drimys lanceolata* in those above 1300 m (4000 ft). Below 1300 m (4000 ft), *Nothofagus cunninghamii*, *Atherosperma moschatum*, the ferns *Dicksonia antarctica*,

Blechnum procerum and *Grammitis billardieri* and the bryophytes *Acanthocladium extenuatum*, *Camptochaete ramulosa*, *Dicranoloma menziesii*, *Acrobolbus tenellus* and *Chiloscyphus fissistipus* have the highest probability of occurrence. The low closed forest (above 1300 m, 4000 ft) is further characterized by a large number of herb species of both high (over 75%) and low (24-49%) probabilities and a characteristic group of bryophytes of low (24-49%) probability. The major difference between closed forest 650-1300 m (2000-4000 ft) and tall closed forest 0-650 m (0-2000 ft) is the intermediate probability (50-74%) of shrubs and lianes, the intermediate to low (24-49%) probability of ferns and the intermediate (50-74%) probability of a large number of bryophyte species occurring in tall closed forest, whereas the closed forest is poor in fern, shrub and herb species.

The floristic analysis indicated that the *Notho-*



FIG. 4—The geographical distribution of the three altitudinal associations of *Nothofagus cunninghamii* in Victoria, A-B, C and D corresponding to tall closed forest, closed forest and low closed forest respectively.

fagus cunninghamii–*Acacia melanoxylon* forests of the Otway Ranges were not significantly different from the other main low altitude regions in Victoria even though *Atherosperma moschatum* is absent. The *Atherosperma moschatum*–*Eucalyptus nitens* forest studied on the Errinundra Plateau differed floristically from mid-altitude closed forests in central Victoria chiefly in the absence of *Nothofagus cunninghamii* and the presence of *Telopea oreades* and *Elaeocarpus holopetalus*. This was not, however, sufficient to differentiate this stand from the general closed forest type.

(b) STRUCTURE

The mean height (Fig. 5), form (Fig. 6, 7, 8), density and basal area (Fig. 9) of trees change with increase in altitude. *Nothofagus cunninghamii* in the tall closed forest below 650 m (2000 ft) has a mean height of 37 m (112 ft) and consists predominantly of single stemmed trees. The density of trees is low, and the basal area variable (group A & B in Fig. 9). In the closed forest *Nothofagus* has a mean height of 29 m (90 ft) and is either single or multiple stemmed. The density of trees is greater, and the basal area lower than in the tall closed forest. The low closed forest above 1300 m (4000 ft) has a high density of *Nothofagus cunninghamii* but a low basal area (group D, Fig. 9). The trees are chiefly multi-stemmed and have an average height of 9 m (28 ft). The greatest change in form, therefore, occurs at about 1300 m (4000 ft) (c.f. Fig. 6, 7, and 8). *Atherosperma moschatum* is more or less uniformly sub-dominant in stands up to 1300 m (4000 ft) (excepting the Otways and the Errinundra Plateau) with low densities and basal area and a mean height of 19.6 m (60 ft). At its limit at 1370 m (4200 ft) it is only 3.3 m (10 ft) high. In the Errinundra Plateau

forest (see Fig. 10) it reaches a height, density and basal area comparable with that of *Nothofagus cunninghamii* in analogous stands to the west (see Fig. 9).

The crown cover of the tree species exceeds 75% in all stands and the crowns occupy $\frac{1}{3}$ to $\frac{1}{2}$ of the total tree height. Short horizontal branches are often common on the *Nothofagus cunninghamii* trunk down to ground level. At low altitudes, large swollen burls are present at the base of the *Nothofagus* trees, and these frequently bear numerous shoots. At higher altitudes the burls are not obvious, but the plants readily coppice after damage or death of the main shoot. In all stands a large range of size classes of *Nothofagus cunninghamii* is present, and their frequency distribution suggests strongly that the stand is self-perpetuating.

Atherosperma moschatum has a markedly conical crown in its early stages, but develops an open crown with decumbent lower branches at maturity. Layering commonly gives rise to groups of trees.

Acacia melanoxylon is not common in most stands and is single stemmed with a very distinct crown. Young trees are rare except at the edges of the stand or in large gaps.

In the low closed forest *Leptospermum grandifolium* occurs as single or multi-stemmed trees, and possesses a distinct crown. The density and basal area of this species may be greater than that of *Nothofagus cunninghamii* in the same stand.

CONTROLLING FACTORS

The most consistent environmental factor correlated with *Nothofagus cunninghamii* distribution is the high, uniformly distributed rainfall. *Nothofagus cunninghamii* may be found in all areas in Southern Victoria with rainfall exceeding 150 cm

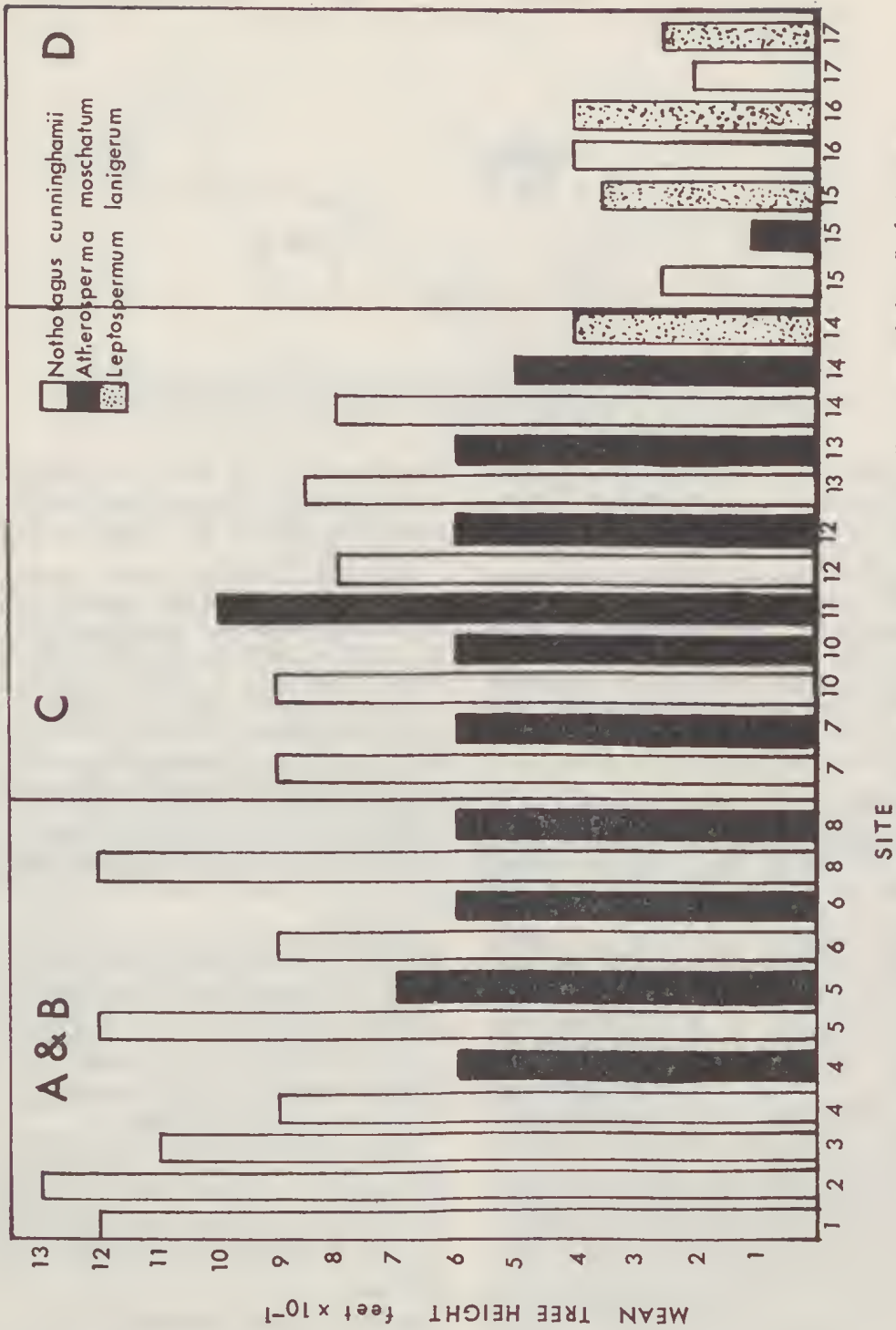


FIG. 5—The mean tree height of each species in each stand, arranged according to association, *L. lanigerum* = *L. grandifolium*, A & B 650 m (2000 ft); C, 650-1300 m (2000-4000 ft); D over 1300 m (4000 ft).

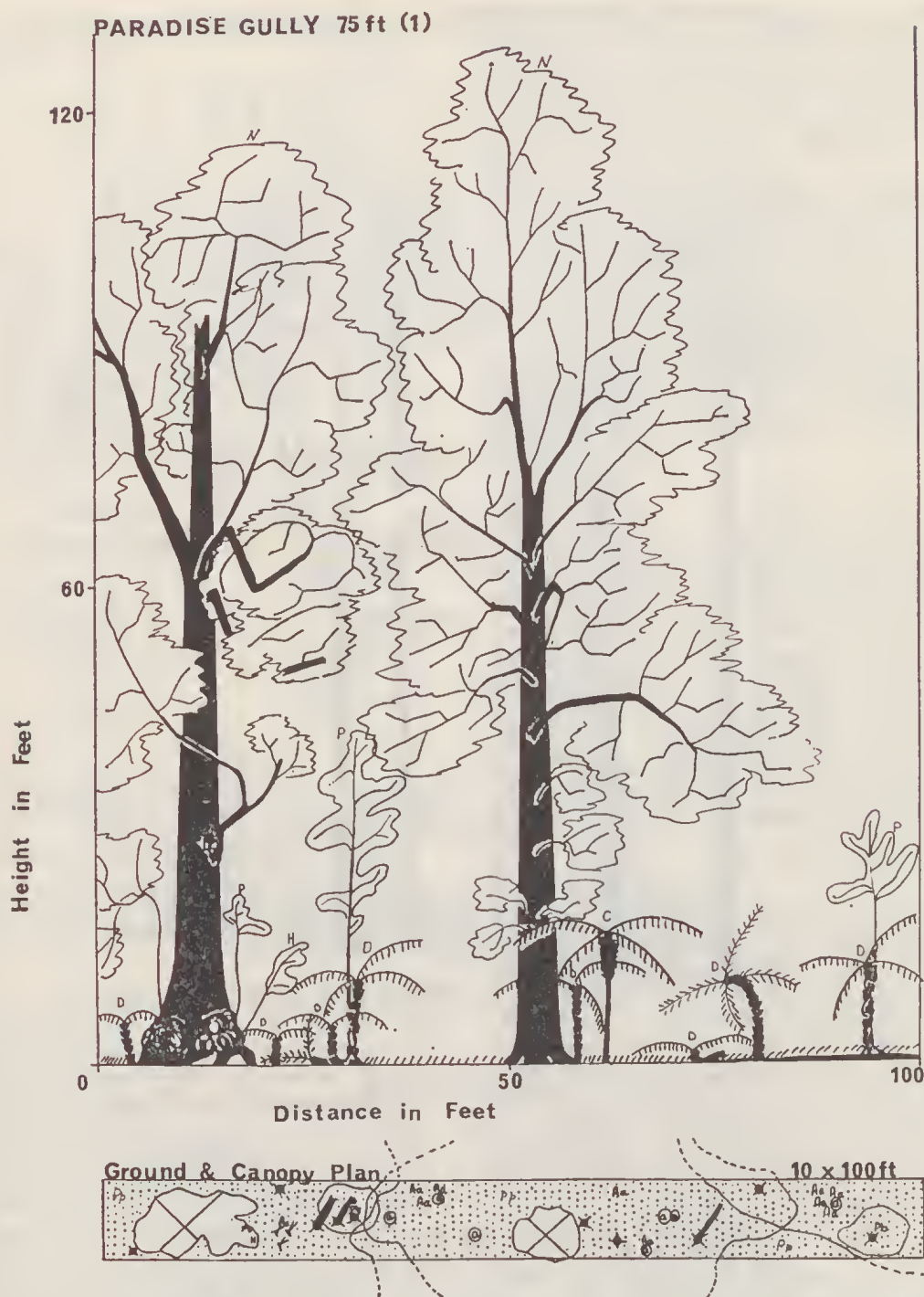


FIG. 6—Plan and profile diagrams of a tall closed forest stand 0-650 m (0-2000 ft). N = *N. cunninghamii*, P = *Prostanthera lasianthos*, D = *Dicksonia antarctica*, H = *Hedycaria angustifolia*.

MT DONNA BUANG 3300 ft (13)
150

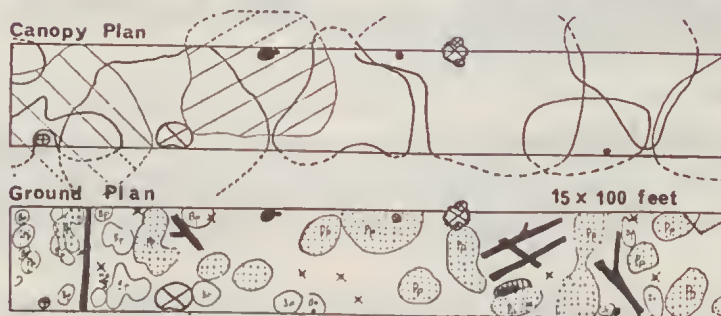
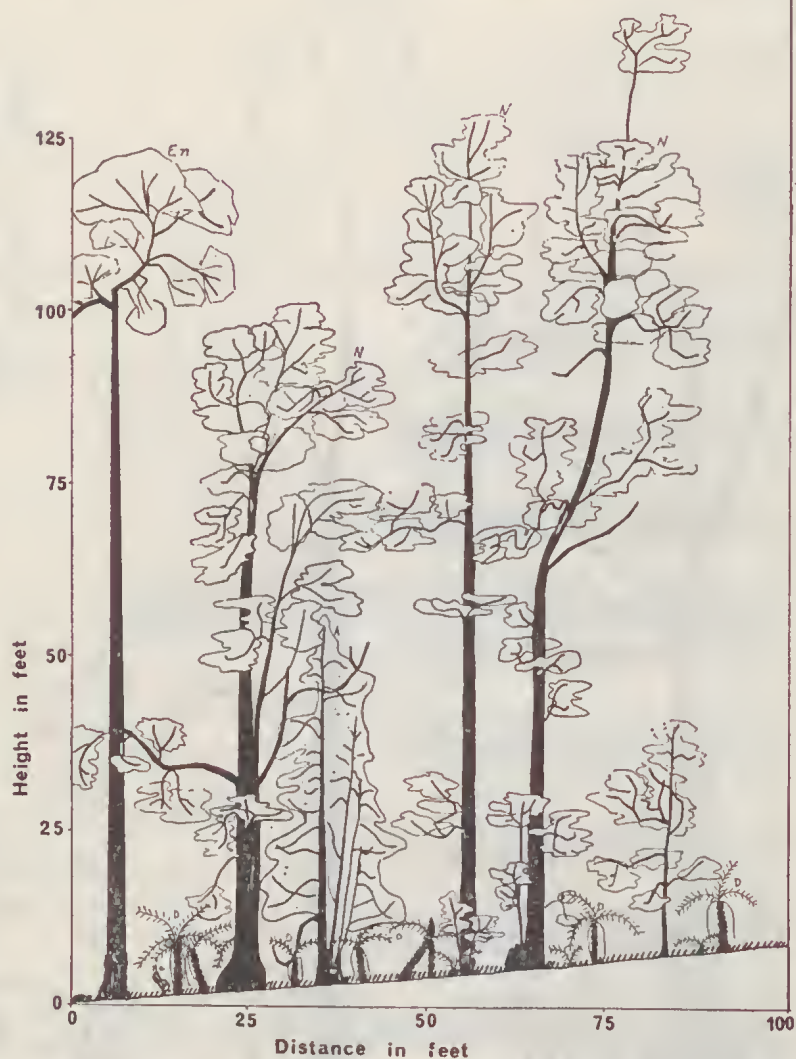


FIG. 7—Plan and profile diagrams of a closed forest stand 650-1300 m (2000-4000 ft). N = *N. cunninghamii*. A = *A. moschatum*, D = *Dicksonia antarctica*, En = *Euc. nitens*.

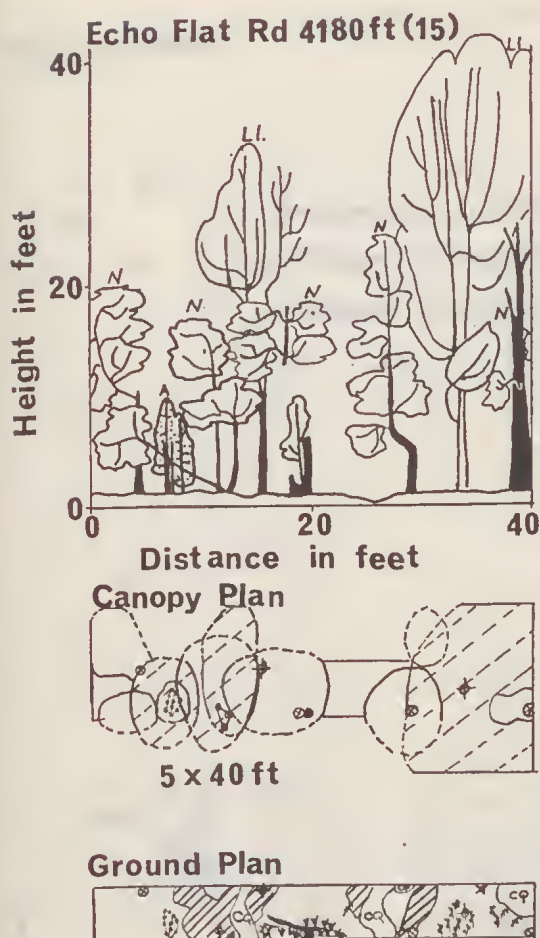


FIG. 8—Plan and profile diagrams of a low closed forest stand 1300 m (over 4000 ft). N = *N. cunninghamii*. A = *A. moschatum*. Ll. = *L. grandifolium*.

(60 ins) per annum, although in sheltered gullies it occurs in rainfalls down to 135 cm (50 ins) per annum. The higher precipitations which occur in the North Eastern Highlands are likely to be less effective due to the lower reliability of summer rainfall. In addition, the intensity of cool changes tends to diminish as they progress E. and N., thus the incidence of low cloud and mist in the summer is likely to be less on the north-eastern mountains than in the Central and Southern districts at equivalent altitudes.

With the increase in altitude the length of the growing season is reduced and the incidence of frost increased. Snow, which is a regular feature of the climate above 1300 m (4000 ft), may lie for several weeks at a time. Below this altitude it becomes more sporadic and is very rare at sea level.

Soil does not appear to be a discriminating

factor in *Nothofagus cunninghamii* distribution. In Victoria it occurs on kraznozems, alpine humus soil, grey loams and colluvial and alluvial soils. The fertility of the soils ranges from moderately low to moderately high. The parent materials giving rise to the soils are chiefly granite, granodiorite, dacite and arkose.

Fire is an important factor controlling the distribution of these forests and they may have been destroyed or greatly reduced in area by the spate of repeatedly severe fires since the advent of white man. *Nothofagus cunninghamii* coppices following moderately severe fires, whereas *Atherosperma moschatum* is killed (Howard 1970). Unquestionably the occurrence of fire promotes the perpetuation of the eucalypt overstorey, and greatly modifies the species composition and microenvironment.

DISCUSSION

The distribution of the three *Nothofagus cunninghamii*-dominated associations can be explained by the relationship of topography to rainfall at different distances from Bass Strait. Little land over 650 m (2000 ft) is present in the Southern Highland areas, hence only the tall closed forest occurs there. In the Central Highlands region few areas occur below 650 m (2000 ft) with a sufficiently high rainfall to support this forest. Hence the absence of tall closed forest in this area. At higher altitudes and lower temperatures, snow lie and shorter growing seasons are probably responsible for the low stature of the trees, the absence of many lowland species and the appearance of many sub-alpine species.

The absence of *Atherosperma moschatum* from the tall closed forest of the Otway Ranges is difficult to explain, because these forests are otherwise very similar to those elsewhere in Victoria and in north-eastern and north-western Tasmania. The lower fire resistance of *Atherosperma moschatum* compared with *Nothofagus cunninghamii* may be one reason for this absence. The Otway Ranges are vulnerable to fire because of their exposure to dry country on their whole north-western flank. Hence widespread fire in the past may have eliminated *Atherosperma*, but not *Nothofagus* or *Acacia melanoxylon*. Although *Atherosperma moschatum* is easily wind dispersed, the nearest seed sources for any recolonization of the Otways are at Mt. Disappointment, 192 km (120 miles) to the north east across a large area of rainshadow, and at King Island 96 km (60 miles) to the south across a deep section of Bass Strait.

Many closely associated cool temperate rainforest areas occur in the central north-eastern and

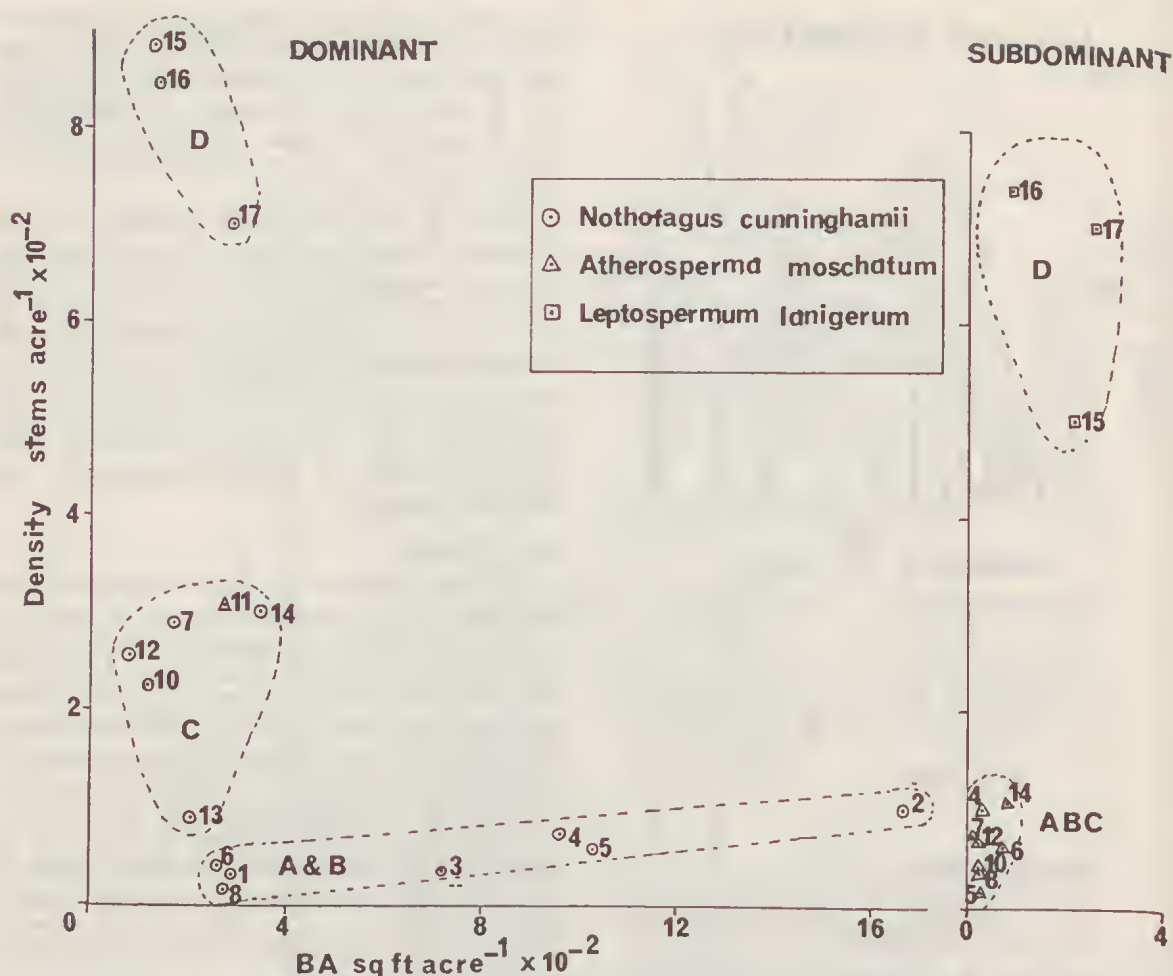


FIG. 9—The relationship between basal area and density in each association for dominant and sub-dominant species. Group A & B, 0-650 m (0-2000 ft) tall closed forest; Group C, 650-1300 m (2000-4000 ft) closed forest; Group D, over 1300 m (4000 ft) low closed forest. Site numbers as in Table 1. *Leptospermum lanigerum* is in the sense of Ewart and now = *L. grandifolium*.

eastern highlands where rainfalls exceed 125-150 cm (50-60 ins) p.a. Below 650 m (2000 ft) in the Central Highlands these are dominated by *Atherosperma moschatum* and *Acacia melanoxylon*. In eastern and north-eastern Victoria cool temperate rainforest is absent below 650 m (2000 ft) and is replaced by a warm temperate facies dominated by *Eugenia smithii* and *Tristania laurina*. Between 650 m and 1300 m (2000 and 4000 ft) in this region the cool temperate rainforest is dominated by *Atherosperma moschatum* alone.

Many gullies dominated by *Atherosperma moschatum* are moist and sheltered throughout the year and the associated species are similar to those in the *Nothofagus*-dominated stands in the same altitudinal zone. In *Atherosperma*-dominated gul-

lies in the Dandenong Ranges where rainfalls are 135 cm (53 ins) p.a., small seedlings of *Nothofagus cunninghamii* were planted in 1967. The subsequent growing season coincided with the worst drought in living memory but *Nothofagus cunninghamii* seedlings survived in both the gully and in the neighbouring moist sites dominated by *Eucalyptus regnans*. These observations suggest that *Nothofagus cunninghamii* is capable of existing in these sites, but establishment from seed would provide the final confirmation of its ability to persist.

Climatic fluctuations during the Quaternary are likely to have greatly affected the distribution of both *Atherosperma moschatum* and *Nothofagus cunninghamii*. Galloway (1971) has recently summed up the available knowledge of the time

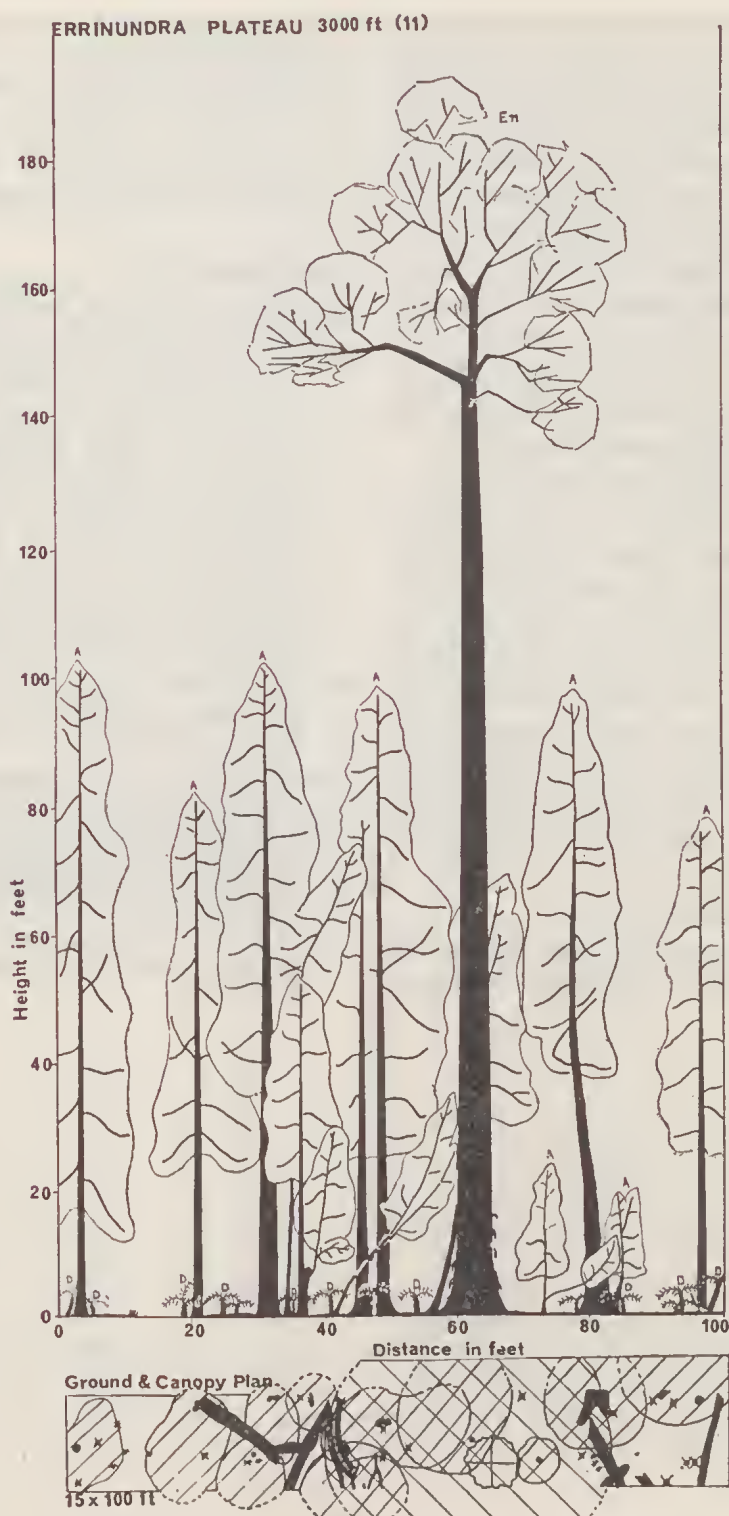


FIG. 10—Plan and profile of *Atherosperma*, closed forest with tall emergent *Eucalyptus nitens* on the Errinundra plateau, East Gippsland. D = *Dicksonia antarctica*.

and type of these changes, and concluded that it is too sparse to act as a guide to pinpointing vegetation changes. However, changes have occurred, and these may have been of sufficient magnitude to cause a contraction of rainforest into the regions in which *Nothofagus* is present today. At the present time at least until pre-white man, *Nothofagus-Atherosperma* forest appears to have been expanding again. The presence of *Atherosperma moschatum*-dominated forests to the E. and NE. of the present distribution of *Nothofagus cunninghamii* may represent the superior ability of *Atherosperma* to disperse seed by wind, enabling it to occupy niches not available to *Nothofagus* because of its inability to cross the rain shadow of the Bairnsdale-Omeo corridor.

Since white settlement, the existing *Nothofagus* forests have been decimated by severe and repeated burning, which may have further arrested *Nothofagus* expansion (Howard & Hope 1970).

In high rainfall areas from near sea level to the lower sub-alpine zone, various closed forests of *Nothofagus cunninghamii* appear to be climax to a number of adjacent open forests dominated by *Eucalyptus* species. The potential limit of such climax in many areas is as yet incompletely known. The dominance of *Nothofagus* over such a wide temperature range may be related to the relative poverty of arboresecent species of the 'antarctic' floristic element (Burbidge 1960) at present in Victoria.

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The distribution of species in *Nothofagus cunninghamii* and allied forests in Victoria arranged to show altitudinal trends. Sites 1, 2, 3, W, and X are in the Otway area, sites U, EP, 6, EB, 7, EF, EG, 10, 12, 13, 14, EI, 15, 16 and 17 are in the Central Highlands, sites 5, 4, and 8 are in the Strzelecki Ranges, site 9 on Wilson's Promontory and site 11 in the Eastern Highlands. Site EP (in the Dandenong Ranges) and site 11 contain no *Nothofagus cunninghamii*.

Sites of Stands	ALTITUDE m and ft	REFERENCE	TREES AND SHRUBS
Paradise Picnic Res.	25 75	1 2 U	Atherosperma moschatum Labill.
Matt's Rest (Reserve)	208 645	234 700	Nothofagus cunninghamii Oerst.
Powelltown	234 700	324 1000	Hedycarya angustifolia A. Cunn.
Calder Riv. (Reserve)	324 1000	324 1000	Coprosma quadrifida (Labill.) Robinson
Hardy's Gully	324 1000	390 1170	Pittosporum bicolor Hk.
Olangelah Dam	390 1170	470 1400	Olearia lirata (Sims) Hutch.
Olangelah River	470 1400	470 1400	Eucalyptus viminalis Labill.
Tarra Valley (Reserve)	470 1400	470 1400	Acacia melanoxylon R.Br.
Jeeralang Creek	470 1400	500 1700	Prostanthera lasianthus Labill.
Beenak	500 1700	570 1700	
Plenty River	570 1700	650 1950	
Cement Creek	650 1950	670 2000	
Bulga National Park	670 2000	750 2250	
Britannia Creek	750 2250	820 2450	
Mississippi Creek	820 2450	960 2880	
Cumberland Falls Res.	960 2880	1000 3000	
Eriundra Plateau	1000 3000	1040 3050	
Mt. Boobyalla	1040 3050	1100 3300	
Mt. Donna Buang	1100 3300	1120 3500	
Mt. Donna Buang	1120 3500	1200 3600	
Tasgerry River	1200 3600	1390 4180	
Echo Flat Road	1390 4180	1470 4400	
Royston Road	1470 4400	1570 4700	
Long Plat	1570 4700		

TABLE 1 (Continued)

REFERENCE	1	2	U	3	EP	W	X	5	4	6	EB	7	9	8	EF	EG	10	11	12	13	14	EI	15	16	17
TREES AND SHRUBS (CONT'D)																									
Pimelea axiflora F.v.M.	X	X																							
Olearia argophylla F.v.M.		X	X	X																					
Pomaderris aspera Sieber ex D.C.			X																						
Acacia dealbata Link.			X											X					X X						
Lomatia fraseri R.Br.								X				X					X X								
Eucalyptus regnans F.Muell									X	X X	X X	X X	X												
Bedfordia salicina DC.										X															
Persoonia arborea F.v.M.												X													
Monotoca sp.													X												
Drimys lanceolata (Poir.) Baill.													X			X X	X X	X			X	X X	X X	X	X
Pimelea drupacea Labill.													X												
Olearia phlogopappa (Labill.) DC.															X		X	X	X						
Acacia frutescens J. H. Willis															X							X			
Correa lawrenciana Hk.																X	X	X			X				
Prostanthera mellissifolia F.v.M.																X X									
Eucalyptus nitens Maiden																X	X	X	X X						
Notelaea ligustrina Vent.																	X								
Tieghemopanax sambucifolius (Sieber ex DC.) Viguer																									

TABLE 1 (Continued)

REFERENCE	1	2	U	3	EP	W	X	5	4	6	EB	7	9	8	EF	EG	10	11	12	13	14	ET	15	16	17	
TREES AND SHRUBS (CONT'D)	25	208	234	1000	324	1170	470	1400	470	1500	570	650	1950	650	2000	750	2450	960	1000	1040	1100	1170	1200	1390	1470	1570
Eucalyptus delegatensis R.T. Bak.																					X	X	X			
Gaultheria appressa A.W. Hill																	X							X		
Telopea oreades F.v.M.																		X								
Leptospermum myrsinoides? Schlecht.																		X								
Elaeocarpus holopetalus F.v.M.																		X								
Coprosma nitida Hk.f.																					X	X	X	X	X	X
Acacia obliquinervia Tindale																					X					X
Leptospermum grandifolium (= lanigerum sens. Ewart) Smith																						X	X	X	X	X
Prostanthera cuneata Bth.																						X	X	X	X	X
Coprosma hirtella Labill.																						X				
Daviesia mimosoides R.Br. var. laxiflora (J. H. Willis) J. H. Willis																						X				
Baeckea utilis F. Muell. ex Mig. var. latifolia (Beth.) J. H. Willis																								X	X	X
Podocarpus lawrencei Hook f. in Hook																										
Epacris paludosa R. Br.																										X

TABLE 1 (Continued)

REFERENCE	1	2	U	3	EP	W	X	5	4	6	EB	7	9	8	EF	EG	10	11	12	13	14	15	16	17
LIANES																								
<i>Clematis aristata</i> R. Br.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Pandorea pandorana</i> (Andr.) Steenis		X	X	X	X																			
<i>Parsonia brownii</i> (J. Britt.) Pichon				X	X			X	X	X	X	X	X	X	X									
<i>Billardiera longiflora</i> Labill.																								
HERBS																								
<i>Australina muelleri</i> Wedd.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Ranunculus hirtus</i> Bks. and Sol.	X											X									X	X	X	X
<i>Carex appressa</i> R. Br.	X						X					X									X	X	X	X
<i>Urtica incisa</i> Poir	X		X					X	X			X							X					
<i>Sambucus gaudichaudiana</i> DC.	X		X	X	X								X			X								
<i>Cynoglossum latifolium</i> R. Br.		X																						
<i>Stellaria flaccida</i> Hook.		X	X																					
<i>Corybas dilatatus</i> (H.M.R. Rupp & W.H. Nicholls) H.M.R. Rupp			X	X																				
<i>Tetrarrhena juncea</i> R. Br.	X								X				X											
<i>Hydrocotyle javanica</i> R.Br.	X										X					X			X		X	X	X	X
<i>Uncinia tenella</i> R. Br.			X	X				X		X	X	X	X		X	X	X	X	X	X	X	X	X	X
<i>Chiloglottis</i> sp.				X																	X	X	X	X

TABLE 1 (Continued)

[illegible]

TABLE 1 (Continued)

[illegible]

TABLE 1 (Continued)

REFERENCE	1	2	U	3	EP	W	X	5	4	6	EB	7	9	8	EP	EG	10	11	12	13	14	EL	15	16	17
FERNS (CONT'D)																									
<i>Hypolepis rugulosa</i> (Labill.) J. Sm.							X													X					
<i>Blechnum minus</i> (R. Br.) Ettingsh.							X																		
<i>Cyathea marcescens</i> N.A. Wakefield							X																		
<i>Sticherus lobatus</i> N.A. Wakefield							X								X										
<i>Todea barbara</i> (L.) T. Moore				X				X																	
<i>Hypolepis australis</i> N.A. Wakefield										X										X					
<i>Blechnum penna-marina</i> (Poir.) Kuhn																						X	X	X	X
FILMY FERNS																									
<i>Hymenophyllum cupressiforme</i> Labill.	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X		X						
<i>Mecodium flabellatum</i> (Labill.) Copeland	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X				X					
<i>Polyphlebium venosum</i> (R. Br.) Copeland		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X					
<i>Mecodium australe</i> (Willd.) Copeland		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X									
<i>Mecodium rarum</i> (R. Br.) Copeland							X				X														
<i>Hymenophyllum peltatum</i> (Labill.) Copeland																					X	X	X	X	X

TABLE 1 (Continued)

REFERENCE	1	2	U	3	EP	W	X	5	4	6	EB	7	8	EF	EG	10	11	12	13	14	EI	15	16	17
LYCOPODS AND PSILOTALES																								
<i>Tmesipteris billardieri</i> Endl.		X		X			X	X																
<i>Lycopodium scariosum</i> Forst. f.																								
<i>Lycopodium selago</i> L.																								
<i>Lycopodium fastigiatum</i> R. Br.																								
<i>Selaginella uliginosa</i> (Labill.) Spring.																								
MOSSES																								
<i>Rhacopilum convolutaceum</i> (C. Muell.) Mitt.	X																							
<i>Goniobryum subbasillare</i> (Hook.) Lindb.	X	X																						
<i>Thuidium furfuraceum</i> (Hook. f. and Wils.) Jaeg.	X			X																				
<i>Papillaria flavo-limbata</i> (C.M. and Hampe) Jaeg.	X	X	X	X	X	X	X	X	X	X	X	X												
<i>Plagiothecium denticulatum</i> (Hedw.)	X						X			X					X									
<i>Rhizogonium distichum</i> (Sw.) Brid.	X			X	X		X	X					X	X	X	X	X	X	X					
<i>Lopidium concinnum</i> H.f. and W.	X	X	X	X	X		X	X	X					X										
<i>Cyathophorum bulbosum</i> (Hedw.) C.M.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X					
<i>Ptychomnion aciculare</i> (Brid.) Mitt.	X	X	X	X		X	X	X	X	X	X	X			X	X			X	X				
<i>Leucobryum candidum</i> (Brid.) H.f. and W.	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X				
<i>Hypnodendron arcuatum</i> (Hedw.) Mitt.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X				

TABLE 1 (Continued)

[illegible]

TABLE 1 (Continued)

[illegible]

TABLE 1 (Continued)

REFERENCE	1	2	U	3	EP	W	X	5	4	6	EB	7	9	8	EF	EG	10	11	12	13	14	15	16	17	
LIVERWORTS (CONT'D)																									
Lophocolea sp.	25	208	234	324	1000	390	470	470	470	500	570	1950	650	670	750	820	960	1000	1040	1100	1170	1200	1390	1470	1570
Frullania rostrata (Hook. f. et. T.) G.L. and N.			X															X		X	X				
Chiloscyphus tridentatus Mitt.			X						X			X	X		X										
Lepidozoea laevifolia Tayl.				X					X		X	X			X			X	X	X	X	X	X	X	X
Gackstroemia weindoferi Herz.			X	X			X	X			X	X	X		X		X			X	X	X	X	X	
Marchantia sp.				X				X							X										
Psiloclada clandestina Mitt.			X																						
Saccogyna sp.			X	X																					
Zoopsis argentia Hook.			X																						
Frullania spp.						X	X	X												X				X	
Frullania falciloba Lehm.							X																		
Balantiopsis convexiuscula Berggr.							X	X	X				X	X			X	X	X	X	X	X	X	X	
Lepidozoea ulothrix (Schwaegr.) G.L. and N.								X				X	X	X	X	X	X	X	X	X	X	X	X	X	X
Bazzania adnexa (L. et L.) Trev.								X				X			X		X	X	X	X	X	X	X	X	X
Leujeunea sp.																									
Chiloscyphus multifolus Steph.									X																
Jamesoniella colorata (Lehm.) Spr.																									
Plagiochila fuscicella (H.f. and T.) Tayl.																X									
Plagiochila circinalis L. and L.																	X								X

TABLE 1 (Continued)

TABLE 2

The per cent probability of species occurrence in three forest types as determined from the similarity analysis. The three probability groups were arbitrarily decided, species occurring in less than 25 per cent of species/site combinations were regarded as non-significant. The sites making up each forest type are: Tall closed forest 0-650 m (0-2000 ft) 1, 2, 3, 4, 5, 6, 8, 9 (Table 1, AB Fig. 3). Closed forest 650-1300 m (2-4000 ft) 7, 10, 11, 12, 13, 14, (Table 1, C Fig. 3). Low closed forest over 1300 m (4000 ft) 15, 16, 17 (Table 1, D Fig. 3).

FOREST TYPE	Tall Closed	Closed	Low Closed
ALTITUDINAL RANGE (ft) (m)	0-2,000 0-650	2,000-4,000 650-1,300	over 4,000 1,300
% PROBABILITY OF SPECIES OCCURRENCE	100-75 74-50 49-25	100-75 74-50 49-25	100-75 74-50 49-25
<u>TREES & SHRUBS</u>			
<i>Nothofagus cunninghamii</i>	-	-	-
<i>Atherosperma moschatum</i>	-	-	-
<i>Drimys lanceolata</i>			-
<i>Leptospermum lanigerum</i>			-
<i>Hedycarya angustifolia</i>	-		
<i>Coprosma quadrifida</i>	-		
<i>Pittosporum bicolor</i>	-		
<i>Clematis aristata</i>	-		
<i>Parsonia brownii</i>	-		
<i>Eucalyptus regnans</i>			-
<i>Acacia dealbata</i>			-
<i>Eucalyptus nitens</i>			-
<i>Telopea oreades</i>			-
<i>Elaeocarpus holopetalus</i>			-
<i>Coprosma nitida</i>			-
<i>Eucalyptus delegatensis</i>			-
<i>Olearia lirata</i>			-
<i>Drimys xerophila</i>			-
<i>Prostanthera cuneata</i>			-
<i>Epacris paludosa</i>			-
<i>Pimelea drupacea</i>			-
<u>HERBS</u>			
<i>Uncinia tenella</i>			-
<i>Viola hederacea</i>			-
<i>Hydrocotyle javanica</i>			-
<i>Libertia pulchella</i>			-
<i>Wittsteinia vacciniacea</i>			-
<i>Fieldia australis</i>	-		
<i>Stellaria flaccida</i>			-
<i>Acaena anserinifolia</i>			-
<i>Geranium pilosum</i>			-
<i>Cotula filicula</i>			-
<i>Gnaphalium</i> sp.			-
<i>Luzula campestris</i>			-
<i>Lagenophora stipitata</i>			-
<i>Carex appressa</i>			-
<i>Chiloglottis</i> sp.			-
<i>Asperula pusilla</i>			-
<i>Hypochoeris radicata</i>			-
<i>Ranunculus hirtus</i>			-
<i>Astelia alpina</i>			-
<i>Hierochloa redolens</i>			-
<u>FERNS & ALLIES</u>			
<i>Dicksonia antarctica</i>	-	-	-
<i>Blechnum procerum</i>	-	-	-
<i>Grammitis billardieri</i>	-	-	-
<i>Hymenophyllum peltatum</i>			-

TABLE 2 (Continued)

FOREST TYPE	Tall Closed	Closed	Low Closed
ALTITUDINAL RANGE (ft) (m)	0-2,000 0-650	2,000-4,000 650-1,300	over 4,000 1,300
% PROBABILITY OF SPECIES OCCURRENCE	100-75 74-50 49-25	100-75 74-50 49-25	100-75 74-50 49-25
<i>Blechnum fluviatile</i>	-	-	-
<i>Polystichum proliferum</i>	-	-	-
<i>Microsorium diversifolium</i>	-		
<i>Asplenium bulbiferum</i>	-		
<i>Polyphlebium venosum</i>		-	
<i>Mecodium flabellatum</i>		-	
<i>Cyathea cunninghamii</i>		-	
<i>Blechnum aggregatum</i>		-	
<i>Blechnum pattersonii</i>		-	
<i>Histiopteris incisa</i>			-
<i>Lycopodium selago</i>			-
<i>Blechnum penna-marina</i>			-
BRYOPHYTES			
<i>Acanthocladium extenuatum</i>	-	-	-
<i>Camptochaete ramulosa</i>	-	-	-
<i>Dicranoloma menziesii</i>	-	-	-
<i>Chiloscyphus fissistipus</i>	-	-	-
<i>Hypnum cupressiforme</i>		-	-
<i>Pterygophyllum dentatum</i>		-	-
<i>Chiloscyphus coalitus</i>		-	-
<i>Riccardia</i> spp.		-	-
<i>Acrobolbus tenellus</i>		-	-
<i>Umbraculum flabellatum</i>		-	-
<i>Atrichum ligulatum</i>		-	-
<i>Cyathophorum bulbosum</i>		-	-
<i>Hypnodendron arcuatum</i>		-	-
<i>Leucobryum candidum</i>		-	-
<i>Papillaria flavo-limbata</i>		-	-
<i>Ptychomnion aciculare</i>		-	-
<i>Plagiochila fasciculata</i>		-	-
<i>Schistochila lehmannia</i>		-	-
<i>Symphyogyna</i> sp.		-	-
<i>Trichocolea australis</i>		-	-
<i>Catagonium politum</i>		-	-
<i>Metzgeria</i> sp.		-	-
<i>Chiloscyphus echinellus</i>		-	-
<i>Lophocolea</i> sp.		-	-
<i>Plagiochila</i> sp.		-	-
<i>Plagiochila circinnalis</i>		-	-
<i>Breutelia elongata</i>			-
<i>Hypnum cupressiforme</i> var. <i>filiforme</i>			-
<i>Leptostomum inclinans</i>			-
<i>Rhizogonium mnioides</i>			-
<i>Frullania</i> sp.			-
<i>Lepidozoea obtusiloba</i>			-
<i>Lepidozoea novae zelandiae</i>			-
<i>Lophocolea semiteres</i>			-
<i>Lophocolea bidentata</i>			-

LOWER DEVONIAN CONODONTS FROM LOYOLA, VICTORIA

By B. J. COOPER*

ABSTRACT: Nineteen disjunct conodont species are recorded from the limestones at Loyola, near Mansfield, Victoria. One new taxon, *Spathognathodus trilinearis* is proposed. The conodont faunas suggest an age close to the base of the Emsian. Correlations are made with conodont faunas previously described from the Coopers Creek Formation and the Lilydale Limestone.

INTRODUCTION

The Loyola limestones are exposed at Loyola, about 200 km NE. of Melbourne and 11 km SW. of Mansfield. Almost all previous geological studies in the area have concentrated on the phosphate or limestone deposits and their associated fossils.

The first reference to the limestone was made by Couchman (1887), with preliminary identification of the fossil content. Subsequent important contributions to the palaeontology include studies on its corals (Hill 1939, Pedder 1967a, 1967b) and stromatoporoids (Ripper 1938).

Howitt (1906, 1923) in his study of the phosphate deposits, mapped the approximate positions of the Old Lime Kiln, Griffiths Quarry and Howes Valley limestone deposits. Bell (1955) mapped all four outcrops and recognized their limited extent.

Fossils from the mudstones associated with the limestones have been described by Chapman (1914, 1915, 1916), Gill (1951, 1969) and Boucot et al (1966).

The present paper deals with the description and stratigraphic significance of the conodont faunas found in the limestones.

STRATIGRAPHY

The area under consideration contains a marine sequence through part of the Lower Devonian. Broad extrapolation along strike from the Jamieson area has led most writers to correlate the Loyola limestones with the 'basal conglomerates' of the Walhalla Group on the eastern margin of the Walhalla synclinorium (Talent 1965, Bell 1955).

In the current investigation, fossiliferous grits

and conglomerates were located about 500 m above the limestones at Loyola. These are probably the local equivalent of the Walhalla 'basal conglomerates'.

The limestone itself outcrops in four small lenses. These are shown on Fig. 1 and are described in the Appendix. The separate lenses are approximately aligned along strike and apparently represent discrete carbonate accumulations developed at a particular horizon and separated by terrigenous sediments.

THE CONODONT FAUNA

All four limestone lenses at Loyola were sampled for conodonts and the following amounts processed: Cummins Road limestone 1 kg, Old Lime Kiln 36 kg, Griffiths Quarry 51 kg, Howes Valley limestone 4 kg. Due to the nature of the exposure, sampling at the Cummins Road deposit was restricted. The Howes Valley limestone proved to be barren.

In all about 160 identifiable conodonts were recovered by digestion in acetic acid, followed by separation in tetrabromoethane adjusted to a specific gravity of 2.75. These included the following form species:

- Belodella devonica* (Stauffer 1940)
- B. resima* (Philip 1965)
- B. triangularis* (Stauffer 1940)
- Drepanodus* sp.
- Hindeodella priscilla* Stauffer 1938
- Neoprioniodus bicurvatus* (Branson and Mehl 1933)
- Ozarkodina denckmanni* Ziegler 1956
- O. media* Walliser 1957

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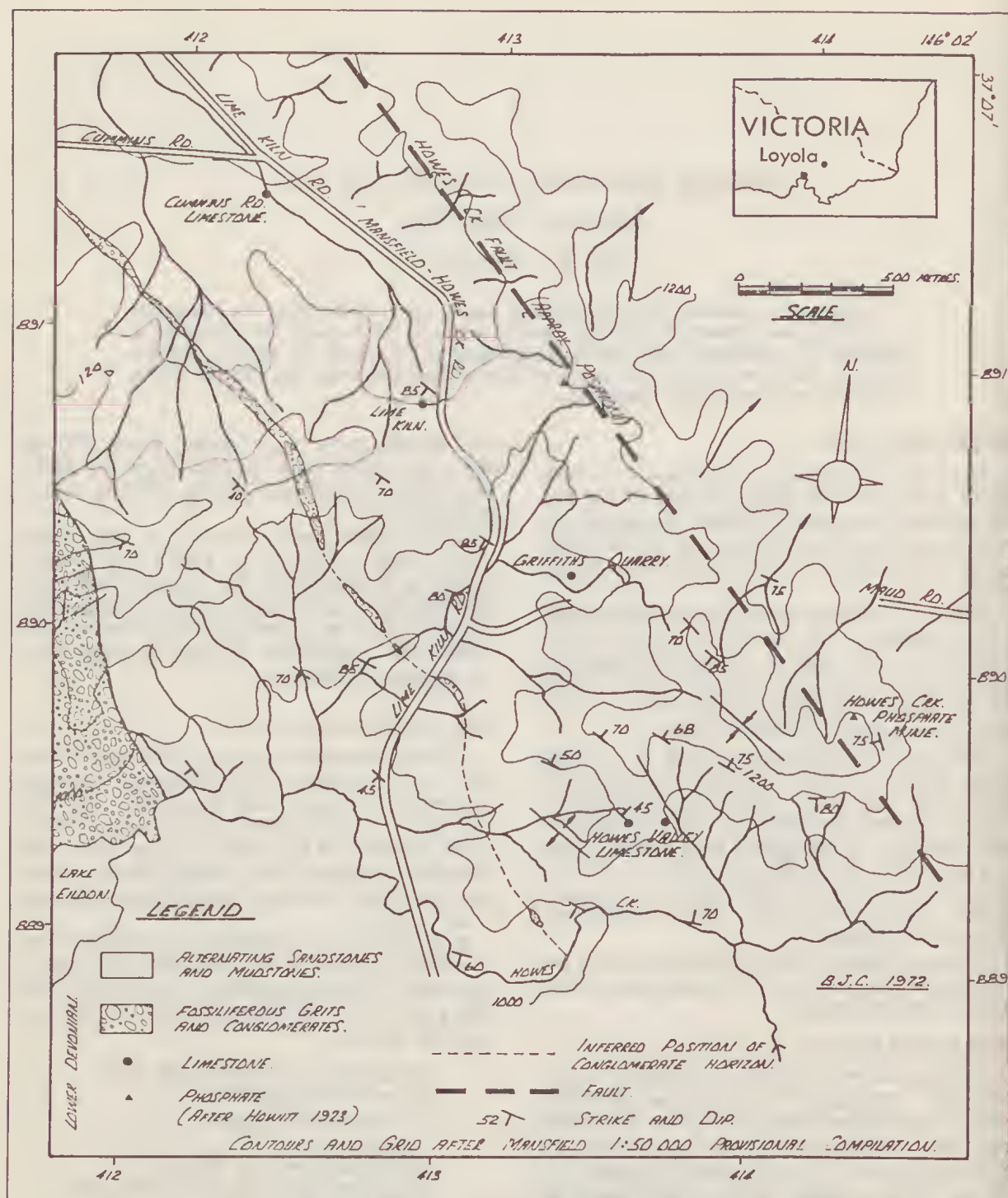


FIG. 1—Map showing Location of the Loyola limestones.

- Panderodus simplex* (Branson and Mehl 1933)
P. unicostatus (Branson and Mehl 1933)
Polygnathus sp.
Scolopodus sp. A
S. sp. B
Spathognathodus inclinatus inclinatus (Rhodes 1953)
S. steinhornensis cf. *buchanensis* Philip 1966
S. trilinearis sp. nov.
Trichonodella inconstans Walliser 1957
T. cf. pinnula Philip 1966
T. symmetrica (Branson and Mehl 1933)

AGE AND CORRELATION OF THE LIMESTONE AT LOYOLA

In the Lower Devonian limestones of Australia Philip and Pedder (1967b, 1967c) recognized a sequence based on tetracorals and conodonts.

The faunas most relevant to the Loyola limestone are:

FAUNA B (*Lyriellasma chapmani* fauna), characterized by the conodont *Spathognathodus sulcatus* (Philip 1965).

Type Locality—Coopers Creek Formation, Tyers, Vic.

FAUNA C (*Zelolasma gemmiforme* fauna), characterized by the conodont *Polygnathus dehiscens* Philip and Jackson 1967.

Type Locality—Cavan Limestone, Taemas, N.S.W.

Philip and Pedder (1967a, 1967b) recorded *Spathognathodus sulcatus* (Philip) (= *Eognathodus sulcatus*) from Loyola and concluded that the limestones belong to the Fauna B horizon.

Conodonts recovered in the present study do not include *S. sulcatus* but a closely related form, *Spathognathodus trilinearis*, has been recognized.

The discovery of a polygnathid at Loyola strongly suggests affinities to Fauna C. In addition, the occurrence of forms almost identical to *Spathognathodus steinhornensis buchanensis* Philip suggest an age younger than Fauna B.

Hence, on the basis of the faunas established by Philip and Pedder (1967b), the Loyola limestone may be assigned to Fauna C.

In relating the Australian sequence to the Rhenish standard, Philip and Pedder (1967a) have maintained an Early Siegenian age for Fauna B and a Late Siegenian age for Fauna C. The elucidation of a sequence of conodont zones by Klapper (1969) in the Lower Devonian of Western North America have indicated that these conclusions should be re-assessed. Klapper's sequence

can be accurately related to a series of brachiopod faunas, which are confidently correlated with the Rhenish type in Europe (Johnson et al 1967, Johnson 1970).

The range of *S. sulcatus* is limited by Klapper to the Middle and Upper Siegenian. The recognition of an older and younger form is based on the size of the basal cavity. Following Klapper, Fauna B would be Middle or Upper Siegenian in age.

Again, according to Klapper (1969) the oldest polygnathid, *P. dehiscens* Philip and Jackson 1970 (= *P. lenzi*) first appears well above the Siegenian/Emsian boundary. Fahraeus (1971) records the discovery of slightly older polygnathids in Nevada, but still within the Emsian. In this framework, Fauna C would be assigned to the Lower Emsian.

The new form, *Spathognathodus trilinearis*, described herein is also important. Specimens of *S. sulcatus* from Tyers, Victoria, approaching this form have been illustrated by Philip (1965 Pl. 10, fig. 25), and Klapper (1969 p. 23) notes similar forms in the Upper Siegenian at Royal Creek, Yukon, Canada.

The Loyola fauna is therefore probably Early Emsian in age, most probably the basal Emsian.

Conodonts from the Lilydale Limestone have been listed and figured by Philip and Pedder (1967a). Unpublished studies by the author indicate that their *Spathognathodus steinhornensis* Ziegler is, in fact, *Spathognathodus philipi* Druce 1970, which is almost identical to *Spathognathodus johnsoni* Klapper 1969. In North America, *S. johnsoni* is indicative of a Lower Siegenian age. With the Middle/Upper Siegenian and Fauna B conodont *Spathognathodus sulcatus* also present at Lilydale, a Lower to Middle Siegenian age is recognized.

Overall then, it can be shown that of the conodont faunas now described from Yeringian limestones, the Lilydale fauna is probably the oldest, followed by the Coopers Creek Formation, at the type locality for Fauna B. The youngest fauna, described herein, is from the Loyola limestone.

SYSTEMATIC DESCRIPTIONS

As the conodont fauna at Loyola was not large, no attempt at recognizing natural conodont species was possible. The following descriptions are therefore based on form taxonomy still used by many workers.

Most of the conodonts recognized at Loyola were well-known Lower Devonian forms, so descriptions of stratigraphically important and lesser known elements only are given.

All specimens are stored in the University of Melbourne, School of Geology Fossil Slide Collection (MUGD.FS).

Genus *Polygnathus* Hinde 1879

Type species: *Polygnathus dubia* Hinde 1879

Polygnathus sp.

(Pl. 2, fig. 3, 4, 5)

DESCRIPTION: A *Polygnathus* having carinae and transverse ridges discernible on the platform. The platform tapers posteriorly and is flexed downward. A prominent basal cavity is present on the aboral surface beneath the platform with grooves extending along the remainder of the unit.

REMARKS: The fragmental and weathered nature of the material prevents positive identification. However, the Loyola form is probably *Polygnathus dehiscens* Philip and Jackson 1970.

MATERIAL: 2 specimens.

Genus *Scolopodus* Pander 1856

Type species: *Scolopodus sublaevis* Pander 1856

REMARKS: *Scolopodus* includes multicostate cones, which are known mainly in Ordovician faunas. However through the years occasional occurrences have been recorded from Devonian strata (Sannemann 1955, Bischoff & Sannemann 1958, Ethington et al 1961, Clark & Ethington 1966). Schulze (1968) correctly suggested that such conodonts were not related to Ordovician forms and went on to describe a lineage from *Scolopodus* to *Icriodus* by way of the intermediate genus *Pelekygnathus*. Klapper and Philip (1971) recognized these three form genera to be part of their Type 4 Apparatuses. *Scolopodus* appears to be rare in all Devonian faunas so far described. Open taxonomy is used in the two forms described here.

Scolopodus sp. A

(Pl. 2, fig. 10, 14)

DESCRIPTION: A species of *Scolopodus* with a gently curved anterior margin. Due to the basal expansion of the unit, the posterior margin is directed anteriorly near the base, followed by a sharp turn posteriorly further up the unit.

The base is poorly elliptical in cross section with one side expanded more than the other. The anterior margin is sharp edged, while the posterior margin has a rounded outline.

The ribs and grooves so characteristic of scolopodids split into a succession of smaller ridges as they approach the expanded base, especially near the anterior margin. All decoration disappears, before reaching the base.

REMARKS: This specimen most closely resembles *Scolopodus devonicus* Bischoff and Sannemann. However, the cross section of the base lacks good symmetry and the anterior margin has less curvature.

MATERIAL: 1 specimen.

Scolopodus sp. B

(Pl. 2, fig. 11, 13)

DESCRIPTION: A species of *Scolopodus* with gently

curved anterior and posterior margins. The whole unit has a sub-circular cross section and is expanded slightly at the base. The external ribbing extends almost to the basal margin, but does not subdivide as in *Scolopodus* sp. A.

REMARKS: The specimen appears to resemble *Scolopodus* sp. (Clark and Ethington 1966), but no illustration accompanies their description. Unfortunately the single specimen found at Loyola was lost, but the form is recorded here for the sake of completeness.

Genus *Spathognathodus* Branson and Mehl 1941

Type species: *Ctenognathus murehisoni* Pander 1856
Spathognathodus steinhornensis cf. *buchanensis* Philip 1966

(Pl. 2, fig. 8, 9, 12; Pl. 2, fig. 2, 3, 4, 5)

cf. *Spathognathodus steinhornensis buchanensis* Philip 1966, p. 450, Pl. 2, fig. 1-15, non fig. 15-28.

cf. *Spathognathodus steinhornensis optimus* Moskalenko 1966, Pedder et al 1970, p. 218, Pl. 38, fig. 4-6, non fig. 7, 10-12.

DESCRIPTION: A *S. steinhornensis* which possesses rather coarse variable denticulation. The basal cavity varies in position, but is usually situated in the central third of the unit. The lateral lobes are slightly asymmetrical.

REMARKS: Pedder et al (1970) believe that *S. steinhornensis buchanensis* is identical with *Spathognathodus optimus* Moskalenko. However, the present writer feels that only the younger form of *S. steinhornensis buchanensis* from the Murrindal Limestone is synonymous, while the older variety from the Buchan Caves Limestone is retained as a separate taxon.

The Loyola specimens differ from ordinary *S. steinhornensis buchanensis* in having greater variation in the position of the basal cavity. They closely resemble *S. steinhornensis eosteinhornensis* (Walliser 1964, Pl. 9, fig. 15; Pl. 20, fig. 7-16, 19-25).

MATERIAL: 36 specimens.

Spathognathodus trilinearis sp. nov.

(Pl. 3, fig. 1, 6, 7)

DERIVATION OF NAME: From L., *tria* = three together, *linearis* = of a line.

DIAGNOSIS: A species of *Spathognathodus* with three rows of denticles in the posterior part of the unit.

TYPE SPECIMENS: Holotype MUGD.FS 1698/15, paratypes MUGD.FS 1698/16, 1698/14, 1714/16.

DESCRIPTION: The unit has a higher anterior blade, which progressively decreases in height towards the 'platform' or three-rowed portion. These anterior denticles are usually aligned with one of the outside rows of nodes on the platform.

The platform does not taper to any great degree in the far posterior of the unit and the troughs between each row of nodes are shallow.

In lateral and aboral views, the species is identical with *Spathognathodus sulcatus* and related forms. The basal cavity is wide and asymmetrical.

REMARKS: This species, together with *Spathognathodus sulcatus* (Philip), *Spathognathodus secus* (Philip), *Spathognathodus linearis* (Philip) and *Spathognathodus irregularis* (Druce), would have been placed in a

separate genus, *Eognathodus* by other workers; see Philip (1965, 1966) and Druce (1970). However, the present writer believes that these forms lie within the diagnosis of *Spathognathodus*, even though the group concerned constitutes an important, closely related branch of the main *spathognathodid* stock.

It has long been recognized that the genus *Polygnathus* must have derived from *Spathognathodus* sometime in the Lower Devonian (Lindstrom 1964, p. 48). The species described here is the closest recorded *spathognathodid* to this genus and indicates the the *S. sulcatus* group gave rise to *polygnathids* at about this time.

The principal differences between *S. trilinearis* and the earliest *polygnathids* are:

1. The continuity of the anterior blade with one of the outer rows of nodes on the platform.
2. The prominent flaring lobes surrounding the basal cavity.

MATERIAL: 4 specimens.

Genus *Trichonodella* Branson and Mehl 1948

Type species: *Trichognathus prima* Branson and Mehl 1933

Trichonodella cf. *pinnula* Philip 1966
(Pl. 3, fig. 10)

REMARKS: The specimen from Loyola differs from type material in the Buchan Caves Limestone (Philip 1966) in having smaller limb divergence (70° – 80°) and longer limbs. However, the laterally flattened cusp and recurved limbs can be easily distinguished.

MATERIAL: 1 specimen.

ACKNOWLEDGMENTS

Dr. G. A. Thomas, Mr. T. A. Darragh and Mr. C. W. Mallett of the School of Geology, University of Melbourne, critically read and suggested many improvements to the manuscript. Mr. R. Britten assisted in the work carried out using the Scanning Electron Microscope.

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APPENDIX

LOCATION OF THE LIMESTONES AT LOYOLA

Previous references to the Loyola limestones are based on a parish plan pre-dating the completion of Lake Eildon. Hence, the deposits are here clearly defined and their location re-described in relation to present roads.

The allotment numbers refer to the Loyola Parish Plan, County of Delatite 1923.

The Grid References (G.R.) are based on 1:50,000 Provisional Compilation for Mansfield.

1. Cummins Road limestone, (G.R. 89134122), near NE. boundary of Allotment 94 or approximately 100 m SE. of the intersection of Cummins and Lime Kiln Roads.

2. Old Lime Kiln, (G.R. 89084127), small quarry with abandoned lime kiln in the SE. corner of Allotment 94 on the western side of Lime Kiln Road, south of Cummins Road.

3. Griffiths Quarry, (G.R. 89034133), quarry in Allotment 132E, filled with water. It is some distance E. of Lime Kiln Road and can be reached via a track leaving the main road.

4. Howes Valley limestone (G.R. 88954137), near western boundary of Allotment 133, almost a km E. of Lime Kiln Road. The limestone occurs in several outcrops on both sides of a ridge, interbedded with fossiliferous mudstones.

EXPLANATION OF PLATES

(All specimens illustrated were photographed using a Graflex camera, having an SM3-CSI attachment on a J.E.O.L. JSM-U3 Scanning Electron Microscope.)

PLATE 2

- FIG. 1—*Hindeodella priscilla* Stauffer 1933. Lateral view of MUGD.FS 1692/15, Old Lime Kiln, $\times 60$.
- FIG. 2—*Drepanodus* sp. Lateral view of MUGD-FS 1695/15, Old Lime Kiln, $\times 60$.
- FIG. 3-5—*Polygnathus* sp. (3) Oral view of MUGD.FS 1710/14, $\times 60$. (4) Oral view of MUGD.FS 1710/16, $\times 60$. (5) Aboral view of MUGD.FS 1710/16. $\times 60$. Both specimens from Griffiths Quarry.
- FIG. 6—*Belodella resima* (Philip 1965). Lateral view of MUGD.FS 1688/21, Old Lime Kiln, $\times 60$.
- FIG. 7—*Ozarkodina denckmanni* Ziegler 1956. Lateral view of MUGD.FS 1694/16, $\times 60$, Old Lime Kiln.
- FIG. 8, 9, 12—*Spathognathodus steinhornensis* cf. *buchanensis* Philip 1966. (8) Lateral view of MUGD.FS 1698/18, $\times 60$. (9) Lateral view of MUGD.FS 1697/15, $\times 60$. (12) Aboral view of MUGD.FS 1696/15 $\times 60$. All specimens from the Old Lime Kiln.
- FIG. 10, 14—*Scolopodus* sp. A. Lateral view of MUGD.FS 1711/16, $\times 60$ and $\times 200$, Griffiths Quarry.
- FIG. 11, 13—*Scolopodus* sp. B. Lateral view, $\times 60$ and $\times 200$, Griffiths Quarry.

PLATE 3

- FIG. 1, 6, 7—*Spathognathodus trilinearis* sp. nov. Lateral, oral and aboral view of holotype. MUGD.FS 1698/15, $\times 60$, Old Lime Kiln.
- FIG. 2-5—*Spathognathodus steinhornensis* cf. *buchanensis* Philip 1966. (2) Lateral view of MUGD.FS 1713/18, $\times 60$, Griffiths Quarry. (3) Lateral view of MUGD.FS 1713/16, $\times 60$, Griffiths Quarry. (4) Aboral view of MUGD.FS 1713/16, $\times 60$, Griffiths Quarry. (5) Lateral view of MUGD.FS 1696/15, $\times 60$, Old Lime Kiln.
- FIG. 8—*Trichonodella symmetrica* (Branson and Mehl 1933). Lateral view of MUGD.FS 1701/13, $\times 40$, Old Lime Kiln.
- FIG. 9, 11—*Trichonodella inconstans* Walliser 1957. Lateral views of MUGD.FS 1699/16, $\times 60$ and MUGD.FS 1699/12, $\times 40$. Both specimens from the Old Lime Kiln.
- FIG. 10—*Trichonodella* cf. *pinnula* Philip 1966. Lateral view of MUGD.FS 1691/16, $\times 120$, Old Lime Kiln.





A COMPUTER SIMULATION STUDY OF MARK-RECAPTURE METHODS IN ECOLOGY

1. Means and empirical standard deviation from four models

By G. ETTERSHANK* AND DAPHNE L. ETTERSHANK*

ABSTRACT: A Fortran computer program is described which simulates an animal population (with births and deaths) subjected to mark-recapture study. All parameters of the study can be specified. The population is estimated by the models of Lincoln, Schnabel, Bailey and Jolly, and mean values and empirical standard deviations are derived on the basis of twenty replications of each set of experimental parameters.

INTRODUCTION

The use of marks on animals to aid the study of their biology is a long-established one. Izaak Walton, in 1653, relates that Sir Francis Bacon attached 'ribands' to young salmon so they could be identified on their return. Marking is often used for the estimation of population size, and a great deal of sophistication has now been brought to the mathematical models used in making such estimates (Cormack 1968).

Considerably less attention has been given to the testing of these models on known populations: such studies have usually involved the comparison of several models on a single population, as, for example, Parr's (1965) study of a population of dragonflies using five models. Phillips and Campbell (1970) used four models on a closed population of whelks on a rocky shore platform.

Manly (1970) simulated populations subjected to mark-recapture methods on a computer, and obtained data on the behaviour of four estimation models. Later (1971a) he examined the behaviour of the variance estimates produced by the method of Jolly (1965) by simulation methods. More recently, other aspects of Jolly's method have been examined (Cormack 1972, Manly 1971b, Carothers, in press), and these are discussed more fully below. A very useful bibliography of mark-recapture methods has been compiled by Anderson (1972); comprehensive discussions are given in Robson (1969) and Seber (1972). White (1971a & b) supplies a Fortran computer program which will handle estimation by Jolly's (1965) method.

Models of mark-recapture estimation are based

on a series of assumptions about the population under study. The accuracy of the estimate will depend to a large extent on how closely these assumptions are met, and on the sensitivity of the particular model to each individual assumption. Thus apart from *sampling* errors, there are also *biological* errors in the estimation process.

The assumptions are as follow:

1. The marking method does not impair the animal functionally or behaviourally.
2. Marks are permanent, unalterable, and accurately decipherable.
3. The return of marked animals into the population does not alter its spatial structure.
4. All animals are equally available for capture, irrespective of
 - (a) mark status (i.e. whether marked or unmarked)
 - (b) age, sex or other group existing in the population (whether distinguishable or cryptic) (i.e. each group is sampled in the same proportion as it occurs in the population)
 - (c) previous capture history (i.e. being captured neither increases nor decreases the probability of an animal's being recaptured subsequently).
5. All parts of the habitat have an equal chance of being sampled.
6. Sampling is carried out in a discrete period of time which is small compared with the total time of the study.

The following assumption is also said to hold for the Lincoln Index and Schnabel models:

7. The population is either closed, i.e. there is

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neither recruitment (births and immigration), nor losses (deaths and emigration) to the population of the period of study; or else recruitment and/or losses can be independently assessed and allowed for.

Assumptions 1 and 2 can be examined by independent laboratory and field studies. It does seem probable, however, that some marking methods must impair the recipient: for example the more radical toe-removal methods used to code small mammals. Such methods are undoubtedly permanent, and unless the animal accidentally loses another toe, are accurately decipherable. Paint-marks used on insects can chip off, or colours can fade. Such marks can be field-tested by using two (or more) separate, independent marks on each animal, thus checking on the long-term reliability of each system. Marking systems should not be of such complexity that human error in reading marks becomes a factor. This can be assessed by having more than one observer independently decipher each mark.

Assumption 3 is a procedural matter, in the hands of the researcher—it requires deep thought into the *timing*, as well as the placement, of releases. It is probably also advisable to release animals at the point of capture, and not to rely on dispersal from one or a few release points.

Before examining the other assumptions more fully, it is necessary to consider the process of estimation (Cormack 1972). The population contains a sub-population of identifiable individuals, the members of which bear either unique, individual marks or a code-mark which identifies the date (and perhaps other information such as place) of marking. It is assumed that the characteristics of this sub-population are known to the biologist (e.g. its size), and that any changes are also known or can be detected (e.g. additions and deletions from the sub-population). Most importantly, it is assumed that changes estimated from this sub-population of identifiable individuals are an estimate (whose accuracy can, in turn, be estimated) of processes in the population. Thus, for each capture-recapture cycle, estimates are

made of sampling intensity \hat{p}_i (in the notation of Cormack 1968)*, birth rate \hat{B}_i , and probability of survival ϕ_i .

From these, further estimates may be made for the overall population, e.g. $\hat{N}_i = n_i \hat{M}_i / m_i$ ($= n_i / \hat{p}_i$)*. Cormack (1972) points out that to solve the estimation formula it is necessary to know (or to directly estimate) one and only one of the sets M_i , p_i , N_i , ϕ_i or B_i ; knowledge of the set ϕ_i or the set B_i must be supplemented by knowledge of one M_i or N_i . From this logical base all the models of mark-recapture estimation can be interpreted. Thus Jolly's (1965) and Seber's (1965)† maximum likelihood solution of the estimation of the marked sub-population is

$$\hat{M}_i = m_i + s_i z_i / r_i$$

where z_i is the number of animals marked before the time of the i th sample, but not included in it; and r_i the number of the s_i animals released at the i th period that are seen later. Thus the second term is an estimate of the number of marked animals alive but unseen at the i th sampling period, and m_i is the number actually seen (Jolly 1965).

On the question of availability of animals for capture, detailed observation may show whether this is likely to be violated. If certain individuals or groups are more conspicuous in the population, their probability of capture may be biased (positively or negatively). Conspicuousness may be physical (e.g. bright plumage or bizarre ornamentation on birds or insects, as in sexual dimorphism), or behavioural (e.g. due to dominance hierarchies or division of labour (Golley & Gentry 1964, Wilson 1971)). Cormack (1972) shows that the catchability of these individuals is higher at the start and thus average catchability declines during the course of the project. However, if the catching method discriminates *against* conspicuous individuals (e.g. by personal bias of an operator, or by a size-filter effect of a trap), the reverse or a different bias may arise.

Another aspect of this same question is trapping history, and trap-proneness and trap-shyness

* $p_i = m_i / \hat{M}_i$

where m_i is the number of individuals of the sub-population of marked animals \hat{M}_i , sampled on the i th occasion

$$\hat{\phi}_i = \hat{M}_i + 1 / (\hat{M}_i + s_i - m_i)$$

where s_i is the number of marked animals released after the i th sample.

$$\hat{B}_i = \hat{N}_i + 1 - \phi_i (\hat{N}_i + s_i - n_i)$$

where n_i is total sample size on the i th occasion, \hat{N}_i is the estimated population at time i .

† Jolly (1965) and Seber (1965) produced the same solutions to the problem of mark-recapture estimates of populations, under a stochastic model; Jolly's treatment, however, is more generalized, and is referred to hereafter.

are well known to workers on vertebrate animals. (The effects of training on invertebrates should not be overlooked, however.) Orians and Leslie (1958) provide a test for random recapture of individually-marked animals. One further situation to be avoided is the use of baited traps in, for example, studies of social insects where recruitment of a specialized group of foragers occurs when a single successful forager has returned to the nest (Wilson 1971). The effects of bias in catchability is reflected in the estimate of M_i ; this is discussed for the Jolly model by Cormack (1972) and Carothers (in preparation).

The bias in estimates caused by differences in survival is discussed by Cormack (1972). In the Jolly method, general survival is estimated for each period; in others (e.g. Fisher & Ford 1947) an overall estimate is made for the entire period, and this may lead to serious bias. The most serious effect of differential survivals will occur when this effect is associated with marking. The situation can be allowed for if the effect is assumed to occur only after the first capture (and marking), and to last only until the next recapture (the type I loss of fisheries biologists) by considering two sub-populations of newly-marked and mature-marked individuals. The estimates then follow logically (Cormack 1972). Manly (1971b) discusses the same situation for the case where animals bear individual marks—he develops a method for analysing type I losses, as a special case of Jolly's estimator (if the animals die while being marked, this is allowed for in the Jolly model).

Assumption 5, that all parts of the habitat have an equal chance of being sampled, rests on the design of the sampling program, which is excellently covered in specialized texts. Planning for efficient sampling will also ensure that assumption 6 is met—that sampling is carried out in a relatively short, discrete time interval.

The present paper presents the results of a computer simulation study in which four estimation models were examined. The selection of these models was influenced by their being used or under consideration for use in studies of the Desert Biome Program of the US/IBP Analysis of Ecosystems. As mark-recapture studies were to be used for a wide range of taxa, a comprehensive, realistic model of a population subject to such study was required. This paper describes the computer model and the first set of results obtained from it, for idealized populations which completely meet the assumptions discussed above.

METHODS

Idealized animal populations, being studied by mark-recapture methods, were simulated by a

program written in Fortran IV called **SYNPOP**. This was run initially on an IBM360/50 computer at New Mexico State University, Las Cruces, New Mexico, and later adapted and expanded for a Burroughs B5500 computer at Monash University.

The basic outline of the program is relatively simple (see Fig. 16). An array '**POP**' is set up, and a number of places in the array—corresponding to the starting or 'seed' value of the population—are set equal to 99, which identifies new-born animals. They retain this value unless they are captured (see later) or killed (when their value becomes zero).

The population then goes through a series of cycles of deaths, births and sampling, the number of cycles being specified by the experimenter. He also specifies death and birth rates, either as probabilities or as fixed fractions of the population at the start of each day, and these may apply uniformly throughout the period of the experiment, or may be specified (independently) in particular cycles. The experimenter may also specify that births should exceed deaths or vice versa; and finally, he may nominate a probability that animals captured in samples, are killed in handling and marking, a common experience in entomological work.

The selection of which animals are killed, and which are sampled (as well as other events of a stochastic nature), is controlled by a pseudo-random number generator which supplies numbers within the population bounds. The appropriate process is then applied to the animal occupying that position in the population array '**POP**' (after a check that that animal is in fact, 'alive'). The pseudo-random number generator has been carefully tested, and supplies a random sequence of real numbers, uniformly distributed in the long run between 0 and 1. This number is multiplied by the standing population size at the time to obtain the order number of the animal selected. The experimenter supplies a set of six random numbers, obtained from one of the published tables (e.g. Rohlf & Sokal 1969) to seed the generator separately for each process.

In each population cycle the population undergoes a death phase first, followed by a birth phase. The numbers of deaths and births are specified by separate sub-routines according to the experimenter's instructions.

DEATH: In the death phase a random number is generated and this animal is examined. If it has a value of 99 its death is recorded; if its value indicates it is a marked animal its mark is recorded in another array '**WLDKIL**'; if its value is zero, this indicates the animal in this array position is dead, and it is ignored for the moment.

In the first two cases the value in the array 'POP' is set to zero, and another random number is obtained. This procedure continues until the required number of deaths has occurred.

BIRTH: In the subsequent birth phase the array 'POP' is checked through and zero spaces are changed to 99 (new-born animals) until the specified number of births has occurred. If there are insufficient zero spaces in array 'POP', its upper bound is increased with new-born animals.

SAMPLING: The array 'POP' is then sampled. Animals are again selected by the random number generator; each is examined and, if dead, another is selected. If the animal has not been previously captured (i.e. equals 99) its value is set to 1. Previously marked animals thus have marks other than 0 or 99—at the start of each cycle, all previously marked animals have their value multiplied by 10 so an animal caught in the previous cycle would, on capture, have a mark of 10. A 1 is then added, and this animal's mark is changed to 11. Similarly, an animal carrying a mark 10101 would have been marked in the present, last but one and last but three cycles. The marks of such previously captured animals (recaptured during sampling) are noted in an array 'MARX', for later printout, and the mark is analysed by the main program (for the Lincoln Index and Schnabel estimators) and by the sub-routines BAILEY and JOLLY for the Bailey Triple Catch estimator (Bailey 1951, 1952) and Jolly's Stochastic estimator (Jolly 1965).

Finally, a random number is drawn; if this is less than the specified probability of an animal being injured during marking, this animal's mark is transferred to another array 'SMPLDD', and its position in the population array 'POP' is set to zero (animal dead). This cycle is repeated until the required size of sample has been obtained.

This sequence of deaths, births and sampling is thus carried out on the population for as many time periods as the experimenter may select. Such a sequence, representing a population over a period of time, is herein referred to as an experiment. For each set of parameters—seed value, birthrate, deathrate, sample size, number of time periods—the experimenter may also nominate the number of times he wishes this experiment repeated independently (or replicated). This is done on the parameter card (see facsimile of printout). For each replicate, the experimenter supplies a new set of six random numbers, as mentioned above, which seed the pseudo-random number generator for probabilistic death or birth functions, random selection of animals for death and capture, variation in sample size, and whether an animal chances to be killed during marking.

Finally, a sequence of different experiments may be carried out in a single run.

The program used here consists of a main program which acquires data (the parameters and random number seeds) and carries out the actual manipulation of the population. There are a series of sub-routines and functions, as follow:

Sub-routine	SAMPLE—calculates sample size
„	BIRTH—calculates number of new animals in each cycle
„	DEATH—calculates number of deaths in each cycle
Function	RNUM—supplies random numbers, n , ($0 \leq n \leq 1$)
Sub-routine	LINC—estimates the population size by the Petersen or Lincoln Index method
„	SCHNAB—estimates the population size by Schnabel's method
„	BAILEY—estimates the population size by Bailey's 'triple- catch' method
„	JOLLY—estimates the population size by Jolly's stochastic method
„	LINCSM—collates the results of the successive Petersen estimates over the several replicates, supplying a mean and standard deviation for each cycle
„	SNBSUM—collates results for Schnabel estimator as above
„	BALSUM—collates results for Bailey estimator as above
„	JOLSUM—collates results for Jolly estimator as above
„	PRINT—organizes output from the four collating sub-routines
„	TRUVAL—prints out summary of true values of populations at the end of each sequence of experiments

A facsimile of the main program and the sub-routines (excluding the last six, book-keeping sub-routines) is reproduced as an Appendix to this paper.

Output is produced on the line printer for each experiment. After identification, all the parameters for the experiment are given. Optionally, for each cycle, there is a summary of population size, number of births and deaths, and size of sample drawn, and the marks of marked animals caught in samples, of those killed in marking, and of those killed 'in the wild' are displayed. (As a further option, the whole population may be

printed out also, but this obviously consumes a lot of paper and is only used in special cases.) The number of animals marked and unmarked, and the percentage marked, is printed, for each cycle.

At the end of each experiment, the four sets of estimates of the population, together with other relevant statistics (e.g. estimated standard deviation) is printed. The unbiased forms of the estimators are used to obtain population size (Cormack 1968).

After all replicates of the experiment have been completed, summaries of the estimates for each model are printed, and a table of the actual population values in each replicate.

RESULTS

Thirteen separate experiments were performed; each had different birth and death rates, as summarized in Table 1. Each experiment was replicated 20 times. The starting value for each population was 1,000, and the sample size 100 ± 10 . The probability that an animal was injured during capture and marking was set at three per cent. Thus experiment 1 to 3 were with stable populations (except for the slight loss due to injury) where birth and death rates were equal. In experiments 4 to 7 the populations undergo simple growth or decay; in 8, 10 and 12 the populations go through a growth and then a decay cycle; and in 9, 11 and 13, the sequence is reversed.

The results for each experiment are summarized graphically (Figs. 1-13). The upper half of each graph shows the results obtained in two replicates, chosen at random, by each of the four estimator models. Below each of these the mean \pm one

standard deviation for all twenty replicates is shown for each sampling period. The use of the standard deviation as a measure of spread is justified if all replicates are plotted (for example, as in Fig. 14, for Jolly estimator in experiment 1) when it will be seen that 60-70 per cent of points lie within the limits of \pm one standard deviation. Superimposed on each graph is the actual trend line of the population, for comparison.

Fig. 15 shows the proportion of the population bearing marks at the end of each sampling period, for each experiment.

DISCUSSION

Of the four estimation models used, two (Lincoln Index and Schnabel) are based on the assumption that there are no gains (through birth and immigration) or losses (by death or emigration) to the population, while the other two models purport to account for these. The mathematical background (including other assumptions) to these is discussed by Cormack (1968) and Southwood (1966); both authors cite a large number of references to field application of these methods, the former being biased toward fisheries applications and the latter toward entomological studies. (Readers should note that Southwood has a number of errors in his mathematical formulae—marring an otherwise excellent discussion.)

Such theoretical models allow biologists to obtain estimates of population size and other population attributes from mark-recapture studies, together with estimates of the standard deviations. Hopefully, this allows the biologist to place confidence intervals on his estimate(s) of the population: that is, he states that he has, say, 95 per cent confidence that the true size of the population lies within (approximately) two standard deviations of the estimated value. Thus Cormack (1968) cites examples of the use of Jolly's (1965) stochastic method, and quotes percentage 'accuracies' achieved.

Models, however, are predicated on assumptions, as are the statistical methods used to elucidate the models. Is it possible that the assumptions are not justified, in which case either the estimated population size, and/or the associated variance estimate, could be misleading? To date, the only way of testing this proposition was by the comparison of different models. If the answers did not correspond, the particular worker made a subjective judgment in favour of one or more models (e.g. Parr 1965).

Manly (1970) approached this problem by computer simulation of a mark-recapture system. Unfortunately the method he used is not clearly

TABLE 1

Experiment	Periods	Birthrate	Deathrate
1	All	0	0
2	All	0.10	0.10
3	All	0.20	0.20
4	All	0.10	0.0
5	All	0.0	0.10
6	All	0.20	0.10
7	All	0.10	0.20
8	1-5	0.10	0.0
	6-10	0.0	0.10
9	1-5	0.0	0.10
	6-10	0.10	0.0
10	1-5	0.20	0.0
	6-10	0.0	0.20
11	1-5	0.0	0.20
	6-10	0.20	0.0
12	1-5	0.20	0.10
	6-10	0.10	0.20
13	1-5	0.10	0.20
	6-10	0.20	0.10

described in the paper. Each population starts at zero and grows over a period of ten 'days'. At the start of each day, births occurred (either 25, 50, 75 or 100), and at the end of each day, deaths occurred, in accordance with one of twelve life tables. Sample size varied from approximately 10 to 95 per cent. There were 96 populations and each was sampled, independently, ten times during each of the last five days giving ten independent sets of estimates of the population. Estimation models used were Fisher and Ford (1947), Jolly (1965) and Manly and Parr (1968).

Manly analyses the results obtained in terms of 'percentage relative bias' (i.e. [estimate-true value]/true value, as a percentage) and mean square error. He found that when its assumptions were met, the Fisher and Ford method gave results similar to the Jolly method and would be useful when sample sizes were small; however, it assumes a constant birth rate which may be unrealistic in a field situation. He was concerned that Jolly's method appeared to give standard error estimates correlated with the estimates to which they relate. Manly and Parr's method gave good results when sample sizes were 'moderately large'. Manly's approach is interesting and innovative; regrettably, it does not yield any sort of statistical tool that can be applied to other authors' work.

A different approach was used in the present study. Conceptually, the population 'lives' in an array of numbered sites in the computer. If an animal dies, its site becomes available to another, or new sites are created if needed to house an increasing population. By keeping account of how many sites are in use (even if some are unoccupied), the program (by use of a pseudo-random number generator) ensures that animals are killed at random, and that all live animals have an equal chance of being sampled. Captured animals carry a mark that can be translated to yield their complete trapping history. A facility to allow for the possibility that a sampled animal is killed in handling was included, firstly because this is realistic, and secondly because Jolly's model allows for this contingency. Sample size is not fixed, but varies between limits, which is analogous to the field situation where the size of sample is often dependent on meteorological, human and logistical factors, operating around the biometrician's design of the sampling program.

Other options were built into the program, so that, given a set of field parameters (approximate population size, birth and death rates, etc.), the population could be simulated and various sampling regimes tried out. In addition, the four sub-routines used in the program to estimate popula-

tions can be detached and applied to actual capture-recapture data.

An element of artificiality is produced by carrying through the entire death phase followed by the birth phase. As a result, in growing populations some of the new-born animals are clustered at the upper end of the array. A process to re-randomize the animals in the array prior to sampling was tried, but as this produced no difference in the population estimates (but appreciably increased the amount of computer time used) this was not incorporated in the final model. This may not, in any event, be important: Jolly (1965) points out that the important point is that the probability of capturing a marked animal must be the same as the probability of capturing any member of the population, and this is not changed by the arrangement used.

The eventual aim of this project is to examine different population and sample size combinations, with several birth rate/death rate combinations, to formulate sets of tables to yield more realistic confidence intervals for the models selected.

POPULATION ESTIMATES

Figs. 1-13, read in conjunction with Table 1, are self-explanatory, and it does not seem necessary to discuss them in detail. Some general conclusions do emerge that are worth amplifying.

1. Bailey's triple catch method never seems to yield particularly satisfactory results. In general, the estimates are not as good as those of the Lincoln index, and this model will be disregarded in the discussion below.

2. Schnabel's method yields excellent results in populations subject to neither birth nor death, or increasing (experiments 1, 4, 6 and, to a lesser extent, the growth phases of other experiments); it will be noted that the standard deviation of the twenty replicates is uniform and reasonably compact (although the standard deviations estimated by the Schnabel model are ludicrously small). This is a most unexpected conclusion as it has always been assumed that recruitment (as well as mortality) would be a source of error (e.g. Ricker 1958, Cormack 1968). Certainly the model, apparently, does not detect mortality: as will be seen in experiments 2 and 3, the model predicts a growing population, while in 5 and 7 it predicts a more or less stable one. Thus if a reliable (preferably independent) estimate of birth and death rates is available, the Schnabel model could provide very good estimates of population size.

3. Lincoln Index and Jolly's estimator generally perform best where the proportion of marked individuals is high (e.g. 5 and 7), in contrast to Schnabel, which performed best where the pro-

portion of marked individuals is low (Fig. 15); an apparent exception is seen in Fig. 1 where prediction by Schnabel was good and the percentage marked was high, but with neither birth nor death the Schnabel model becomes an extended Lincoln estimate. Ricker (1945) claims that the Schnabel estimator has maximum efficiency when a negligible proportion is marked. In this context, note that the Schnabel estimator did not perform as well in experiment 4 as in experiment 6, where the percentage marked was lower (Fig. 15). This is also illustrated in the experiments where the population is declining. For the present regime, where sample size is about 10 per cent or less of the population, there appears to be little to choose between Lincoln Index and Jolly's estimator. However, Jolly's performance is markedly better where birth and death rates are higher—the succession of Lincoln Index estimates show no improvement in performance with time, but the standard deviation for the Jolly estimates is smaller in the last periods than in the first few. (This is most clearly seen in experiment 3.) In addition, the Jolly model provides estimates of birth and death rates (or, more broadly, dilution and loss rates (Southwood 1966)).

4. The variance (or standard deviation) estimates given by the Jolly model are, as Manly (1970) points out, loosely correlated with the estimate to which they apply. This was observed in the present study also, but it is not really surprising. When the true population size is known it is observed that the standard deviation associated with excessively large estimates usually encloses the true population value. In fact, the standard deviations are highly realistic from this point of view, although this would be little consolation to a biologist endeavouring to estimate the population size within a run of several such large estimates of size and standard deviation.

5. It will be observed that the mean of the twenty replicates for all the models follows (with certain exceptions in Schnabel) the true population curve rather well. This suggests that improvements in estimates could be obtained by sub-sampling from populations, where possible, and averaging the estimates rather than relying on point estimates.

Further analyses of the present data are as yet incomplete, for example the relationship between estimates and standard deviations, loss and dilution rates derived by the estimation models. The present study will be broadened by examining the models with different initial population sizes, by using different sampling rates, and by allowing greater variation in sample size, with constant birth and death rates as in experiments 1 to 7.

These should lead to further generalization concerning the validity of the various models.

CONCLUSIONS

For a series of estimates in a mark-recapture study, Jolly's (1965) model gives the most satisfactory results in situations similar to those tested here, as it includes realistic standard deviation estimates and other data. For the special case of a stable closed population, or one undergoing growth, the Schnabel estimator gives excellent results, although its standard deviation estimate is totally misleading. For those cases where multiple or individual marking of animals is difficult (as in many insects) a series of Lincoln Index estimates gives quite satisfactory results.

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DESCRIPTION OF FIGURES 1-16

FIGS. 1-13—These figures summarize the results of experiments 1-13 respectively (see life-history parameters in Table 1). In all cases, the starting value for the population was 1000; sample size was 100 ± 10 ; and the probability of loss during handling was 3%.

The upper half of each figure shows the actual estimates obtained in periods 2-9 in two replicates selected randomly, using (left to right) the Lincoln, Schnabel, Bailey and Jolly models. Where estimates exceed the limits of the scale (shown on the right) the estimate is shown in numbers.

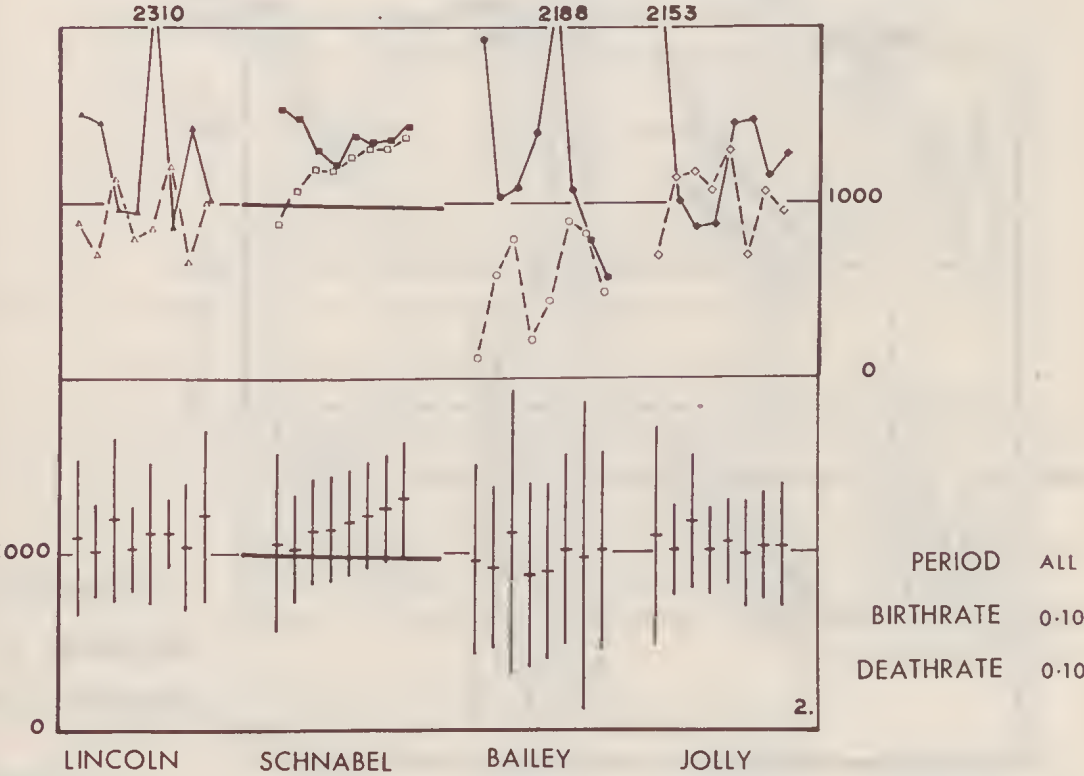
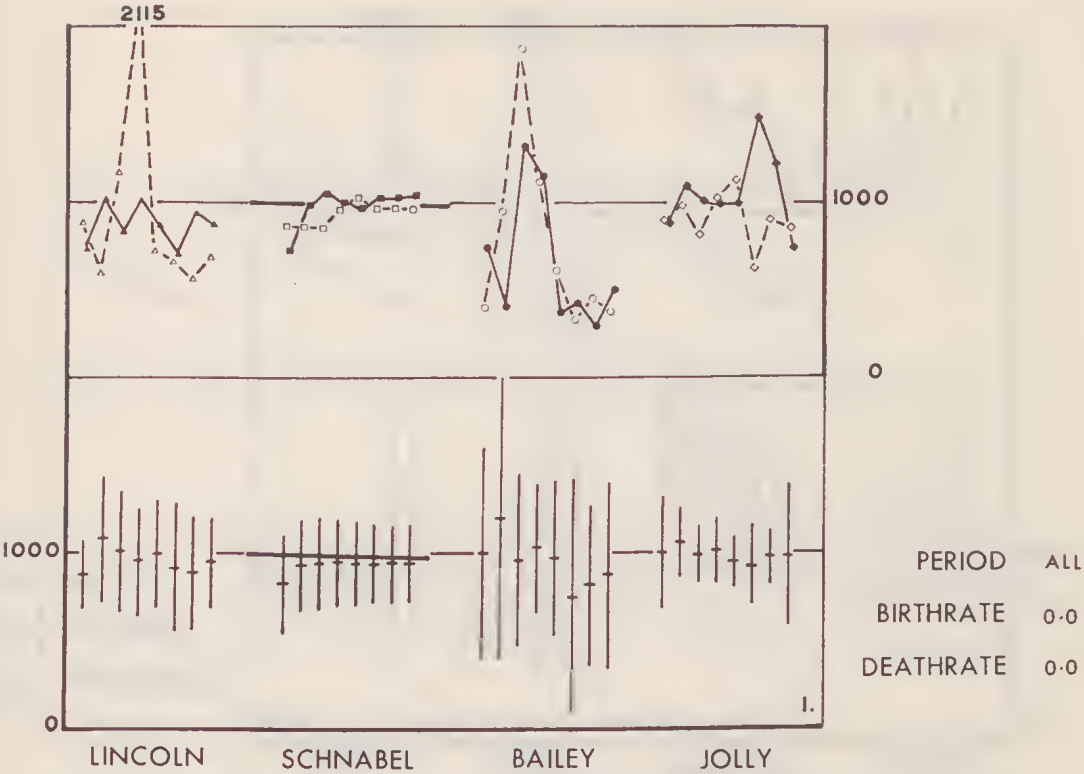
The lower half of each figure (left hand scale) shows the mean (horizontal bar) ± 1 standard deviation (vertical bar) over the twenty replicates, using the same models.

The solid line shows the actual population trend.

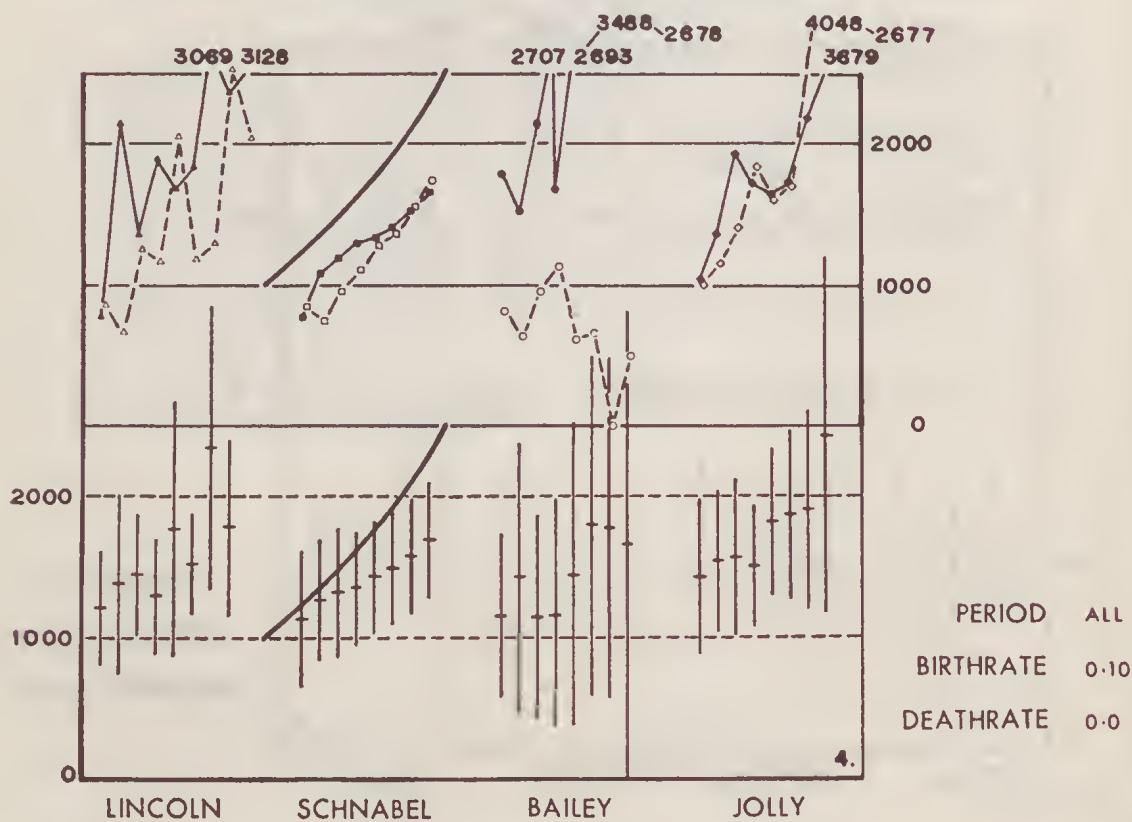
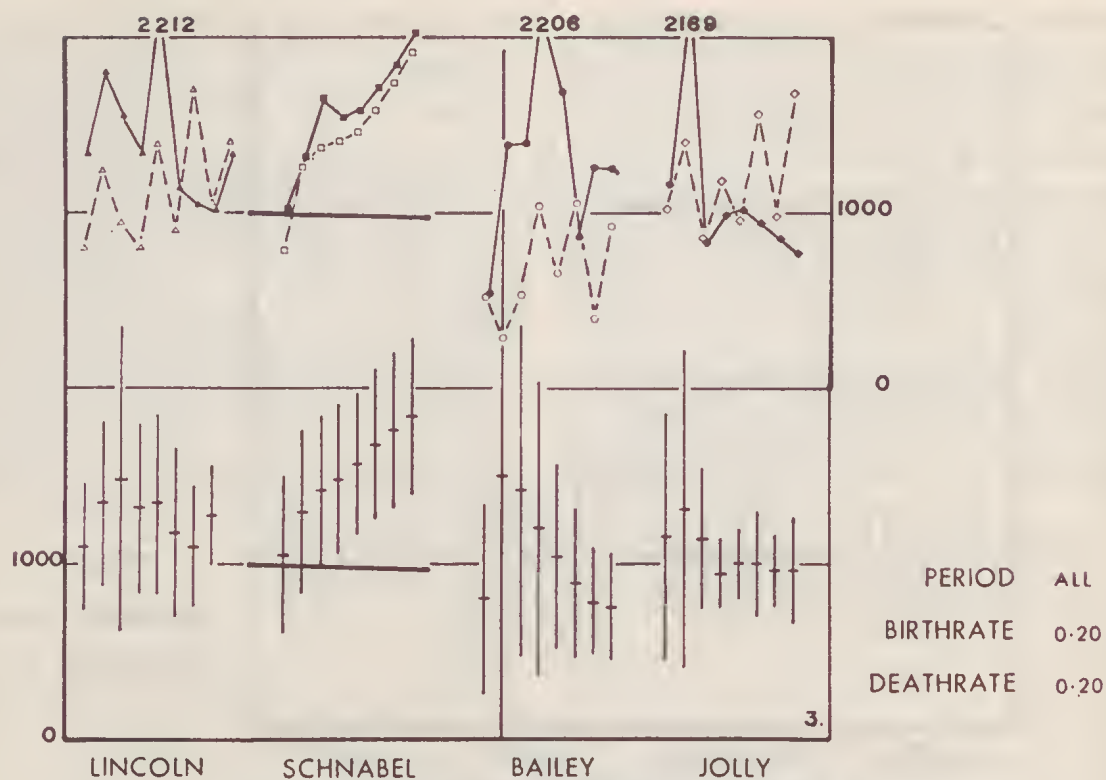
FIG. 14—Distribution of estimates by Jolly model for births = deaths = 0. Each point represents an estimate in the appropriate period, the horizontal bar the mean, and the vertical bar ± 1 standard deviation.

FIG. 15—Percentage of marked individuals, by time periods, for each of the experiments 1-13.

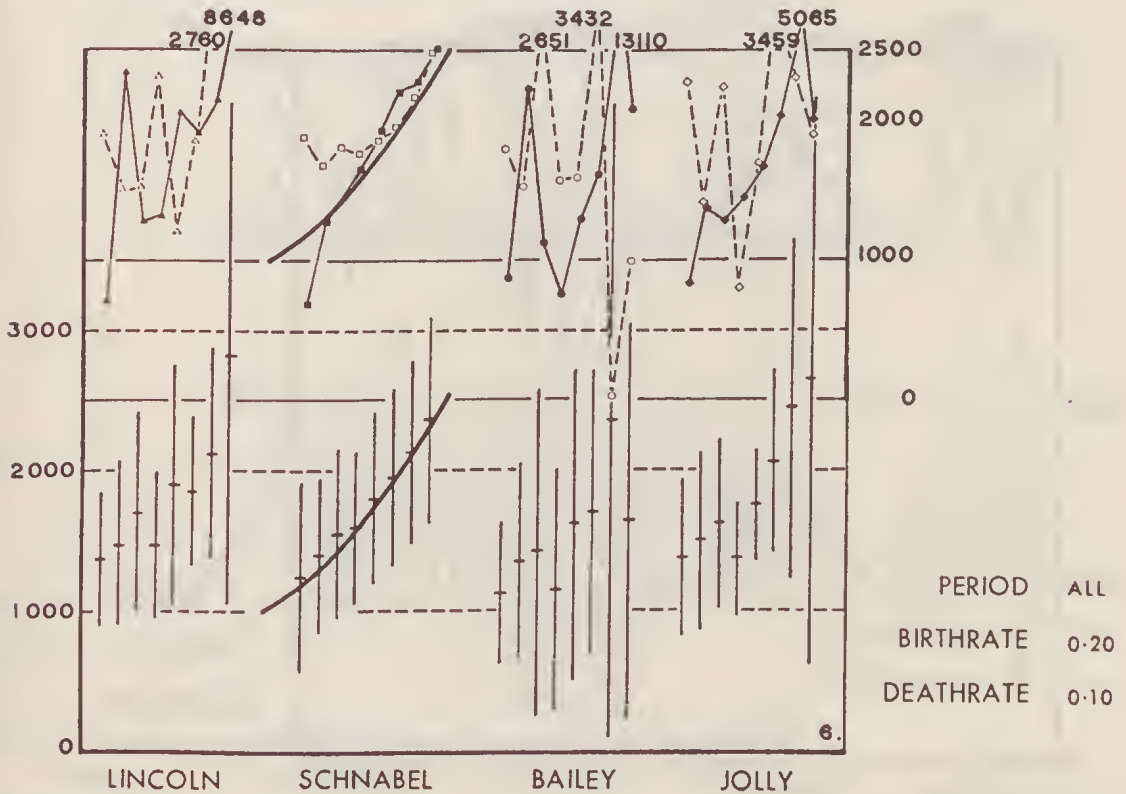
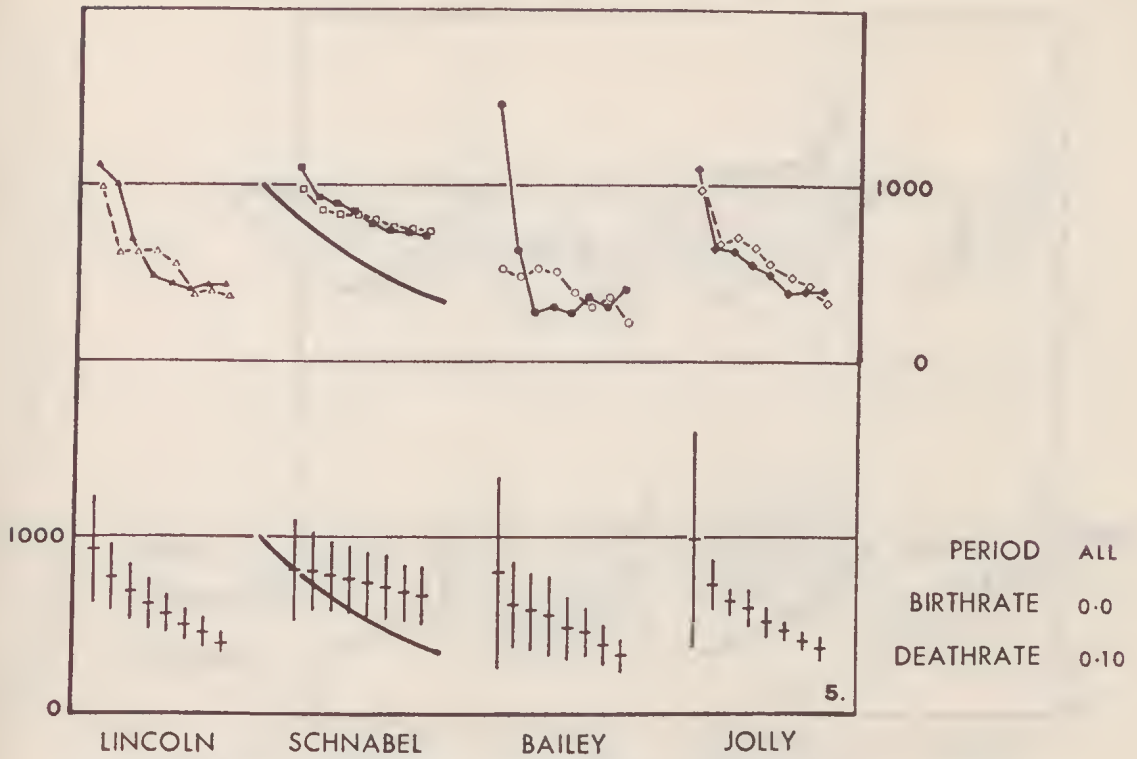
FIG. 16—Flow diagram of main program.



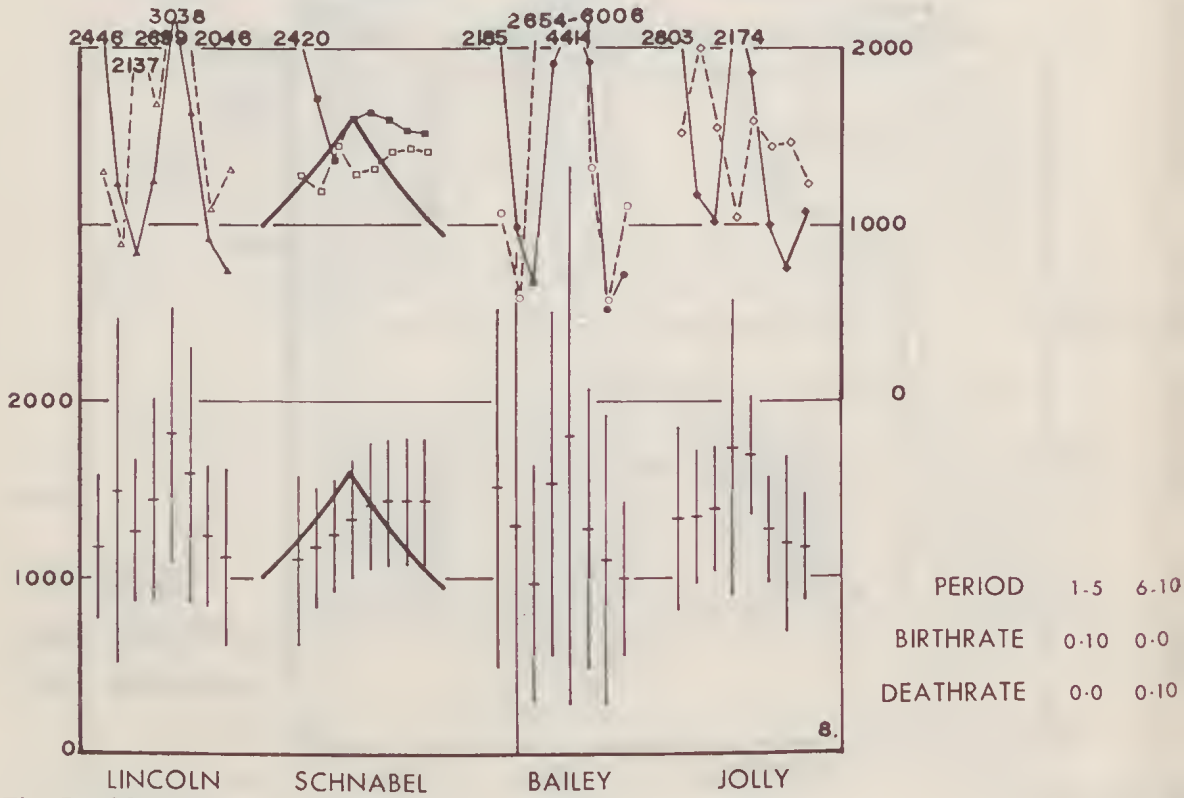
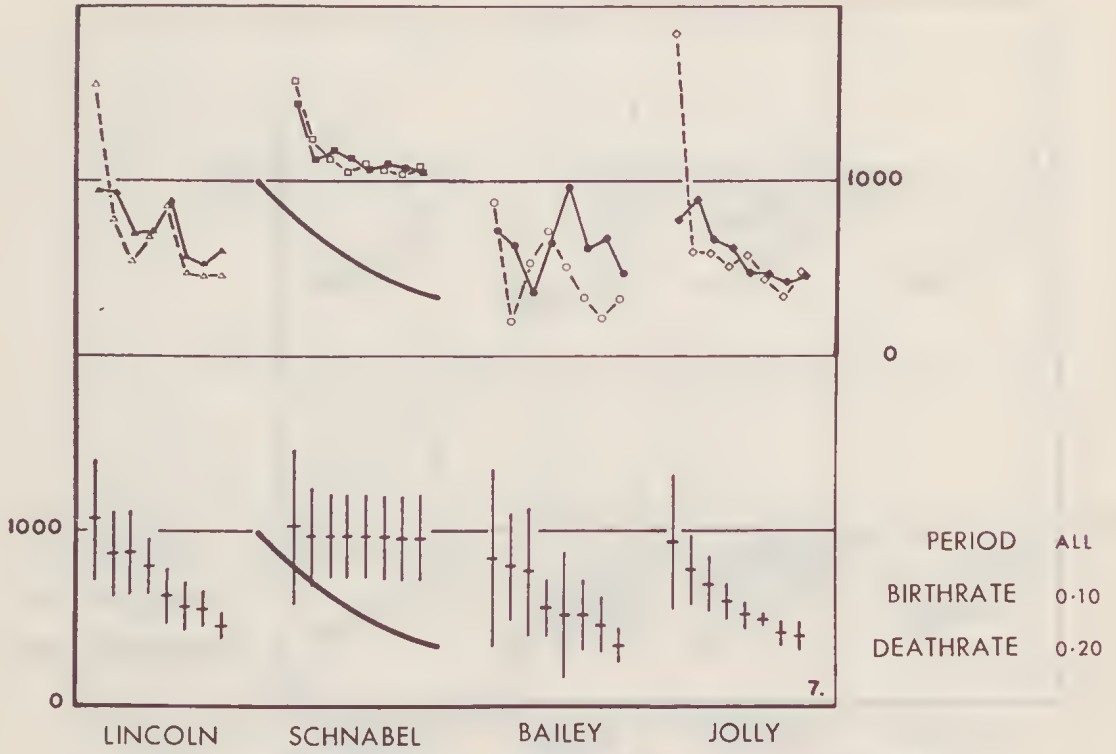
Figs. 1 and 2



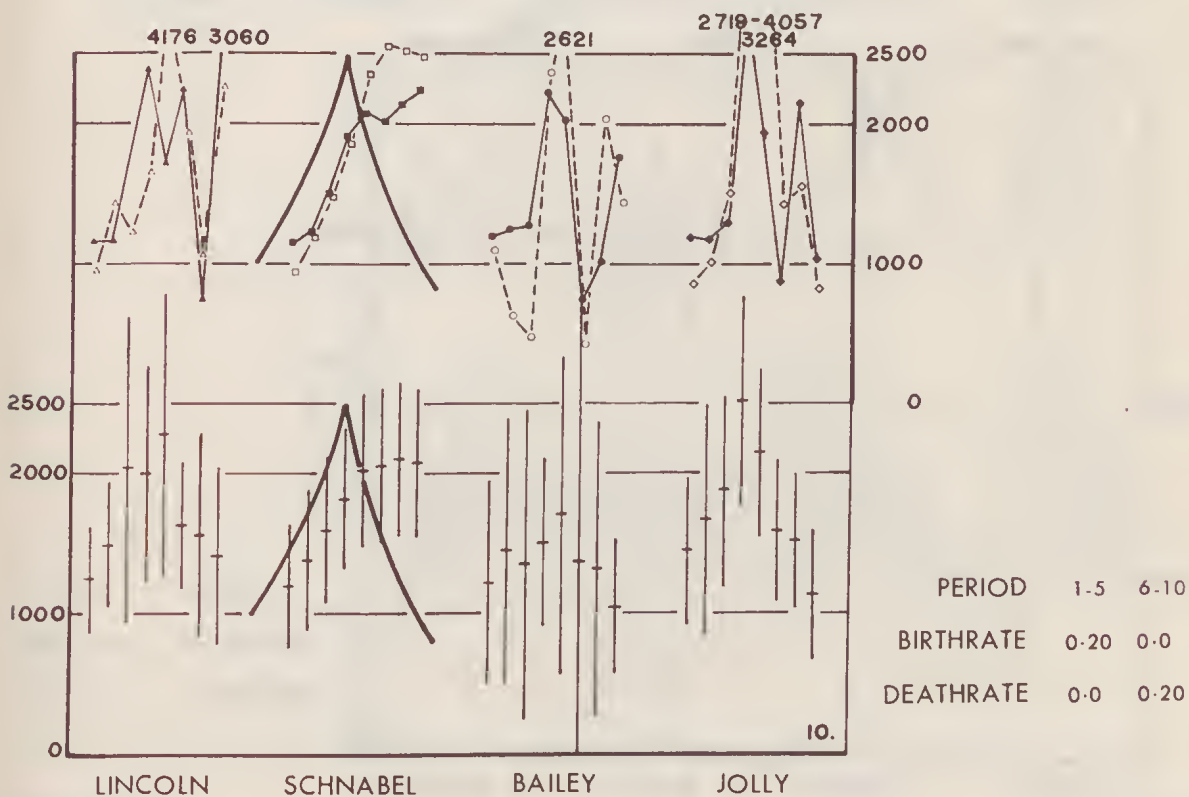
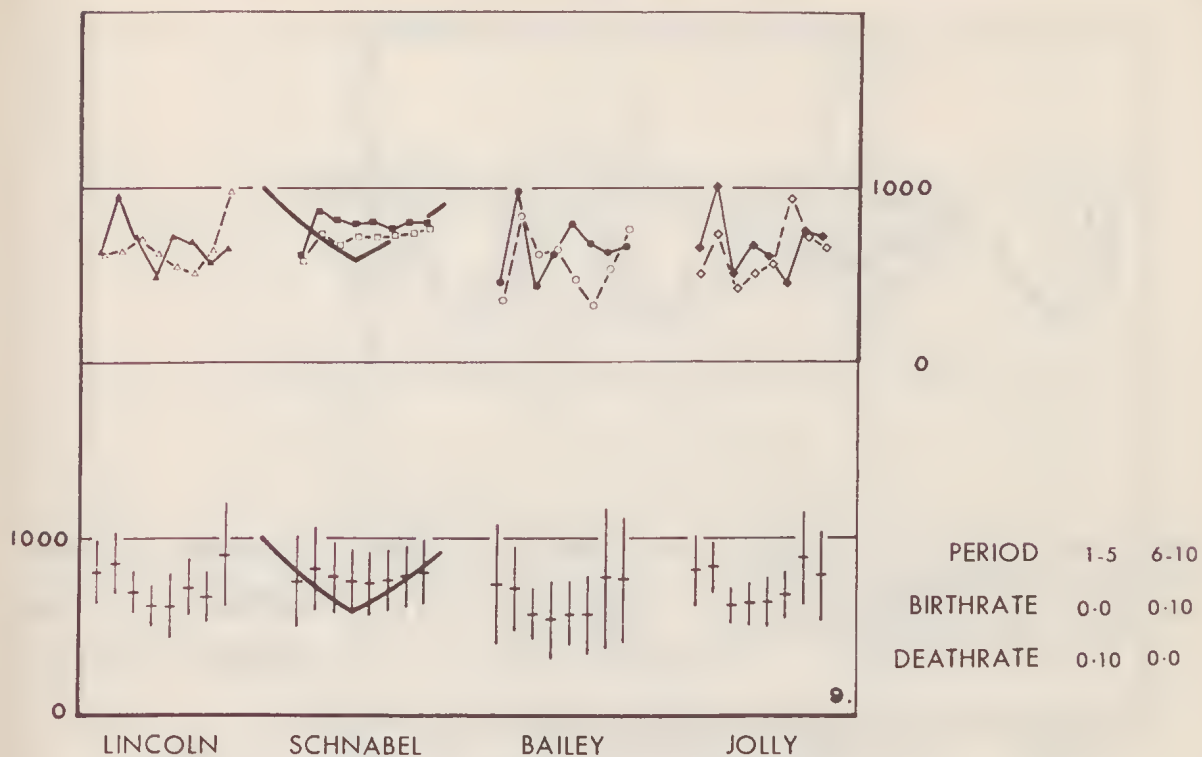
Figs. 3 and 4



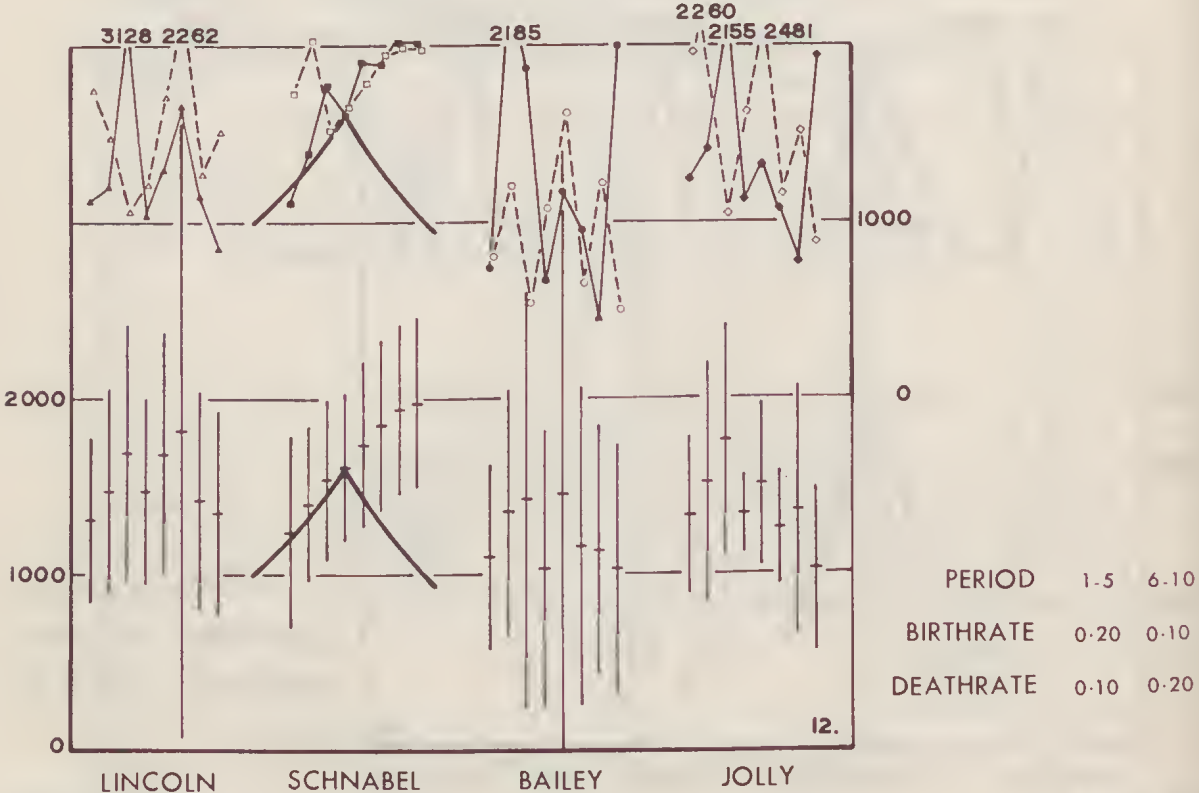
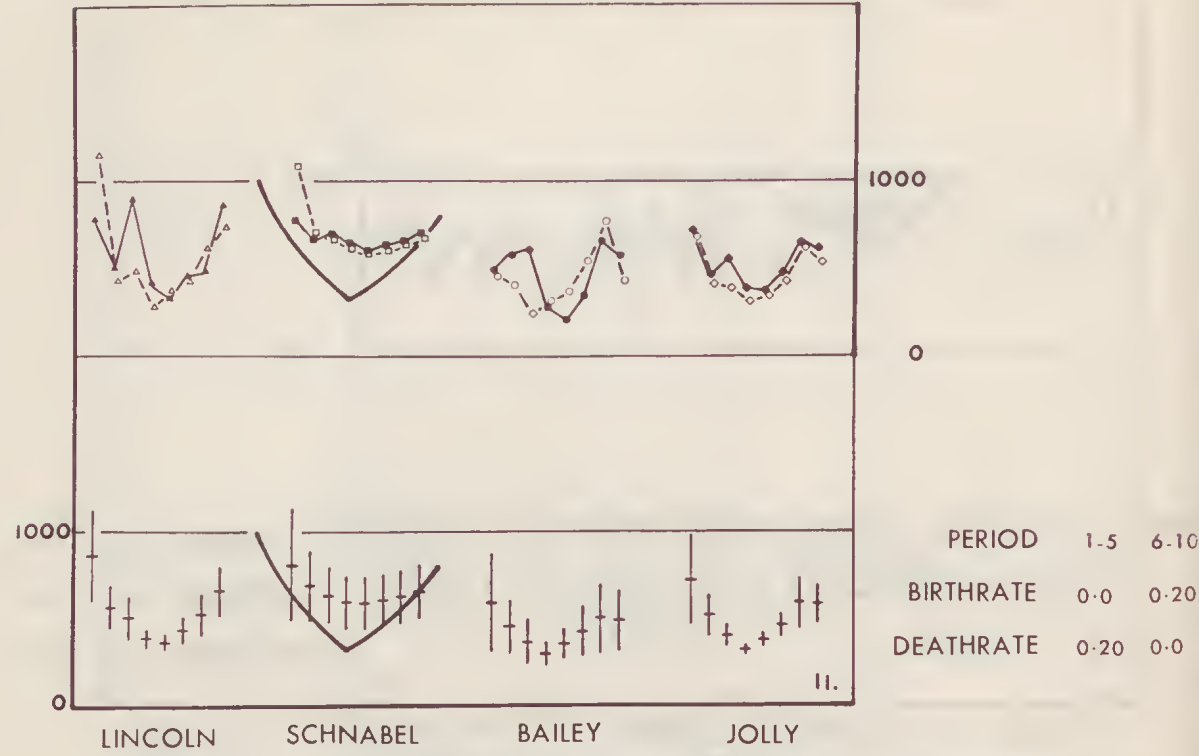
Figs. 5 and 6



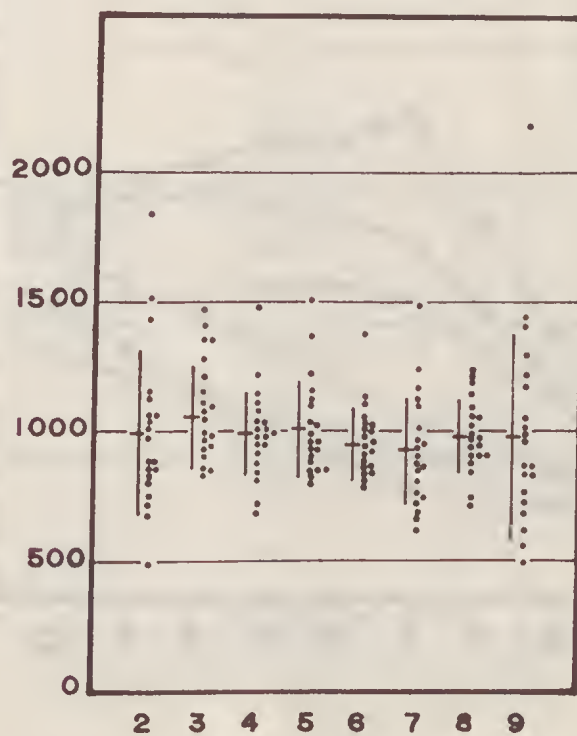
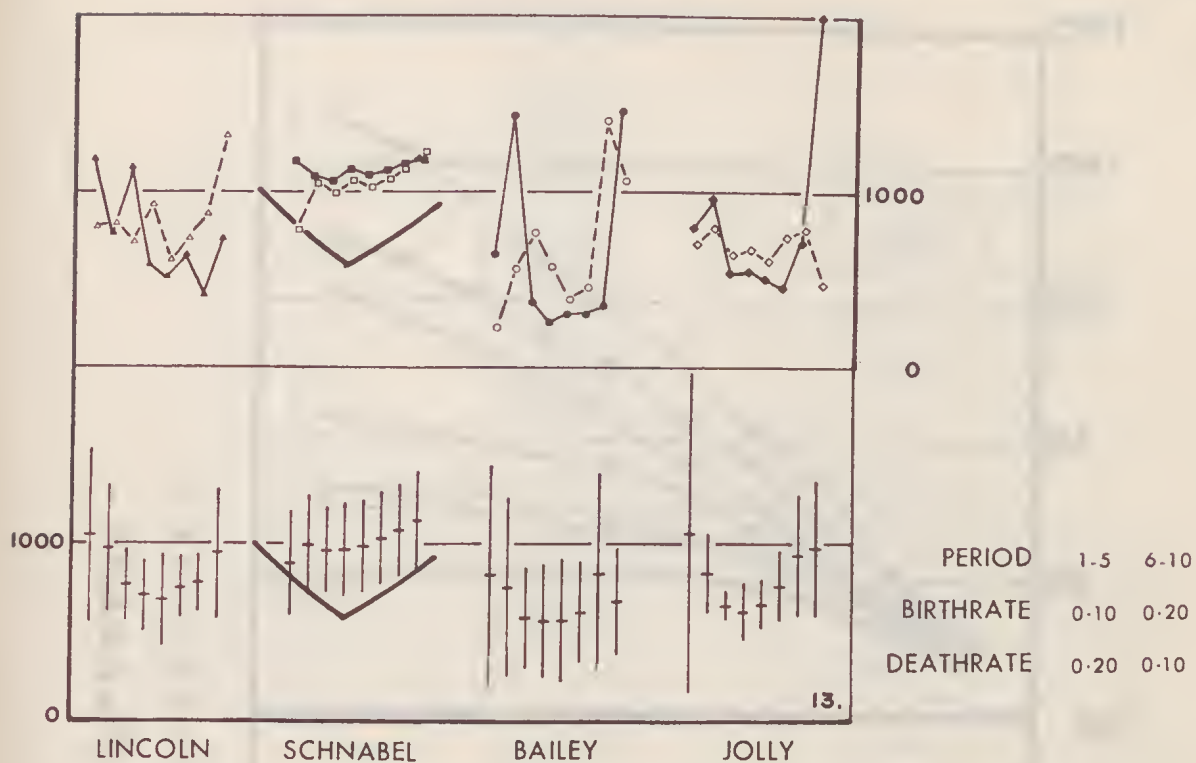
Figs. 7 and 8



Figs. 9 and 10



Figs. 11 and 12



Figs. 13 and 14

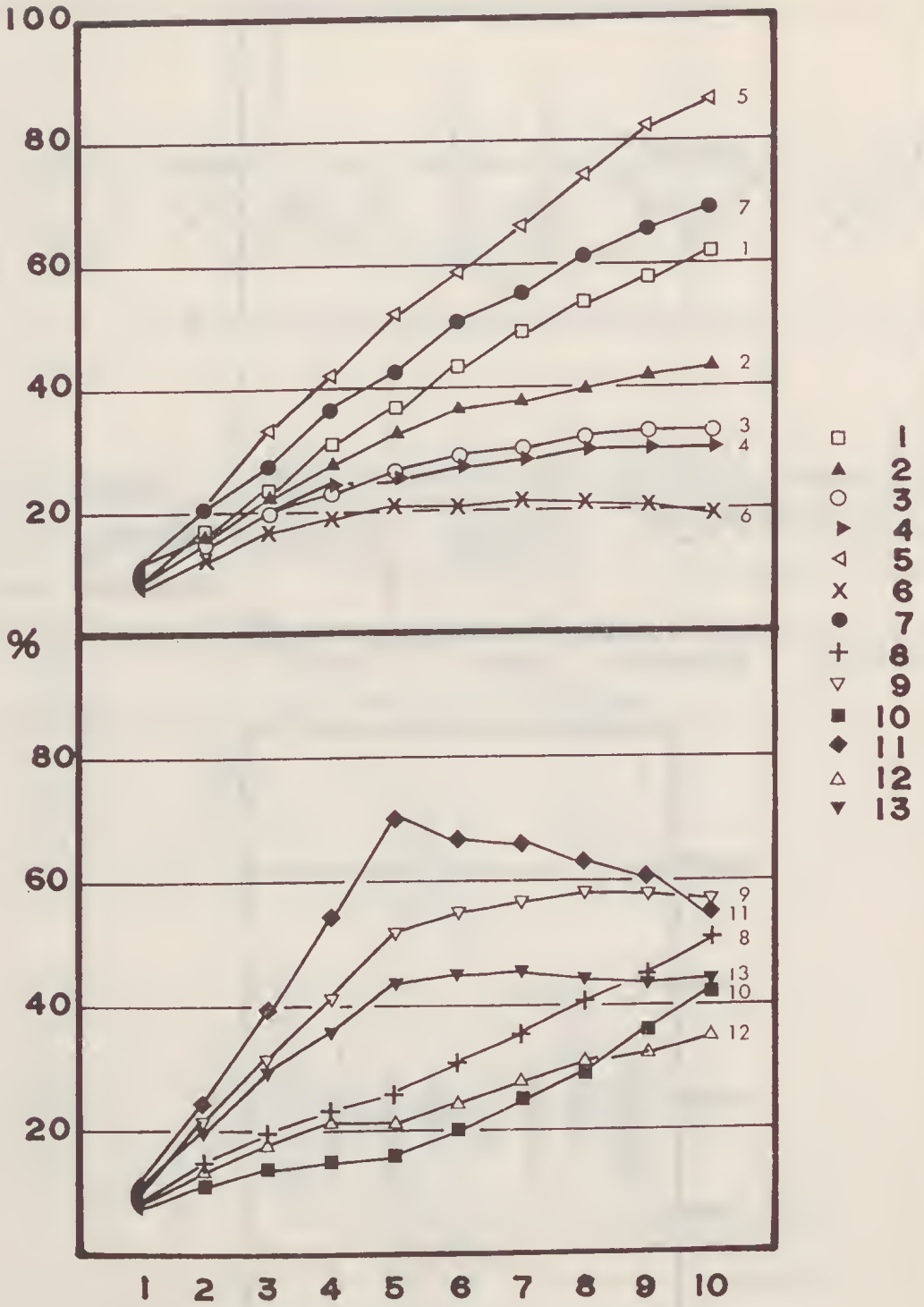


Fig. 15

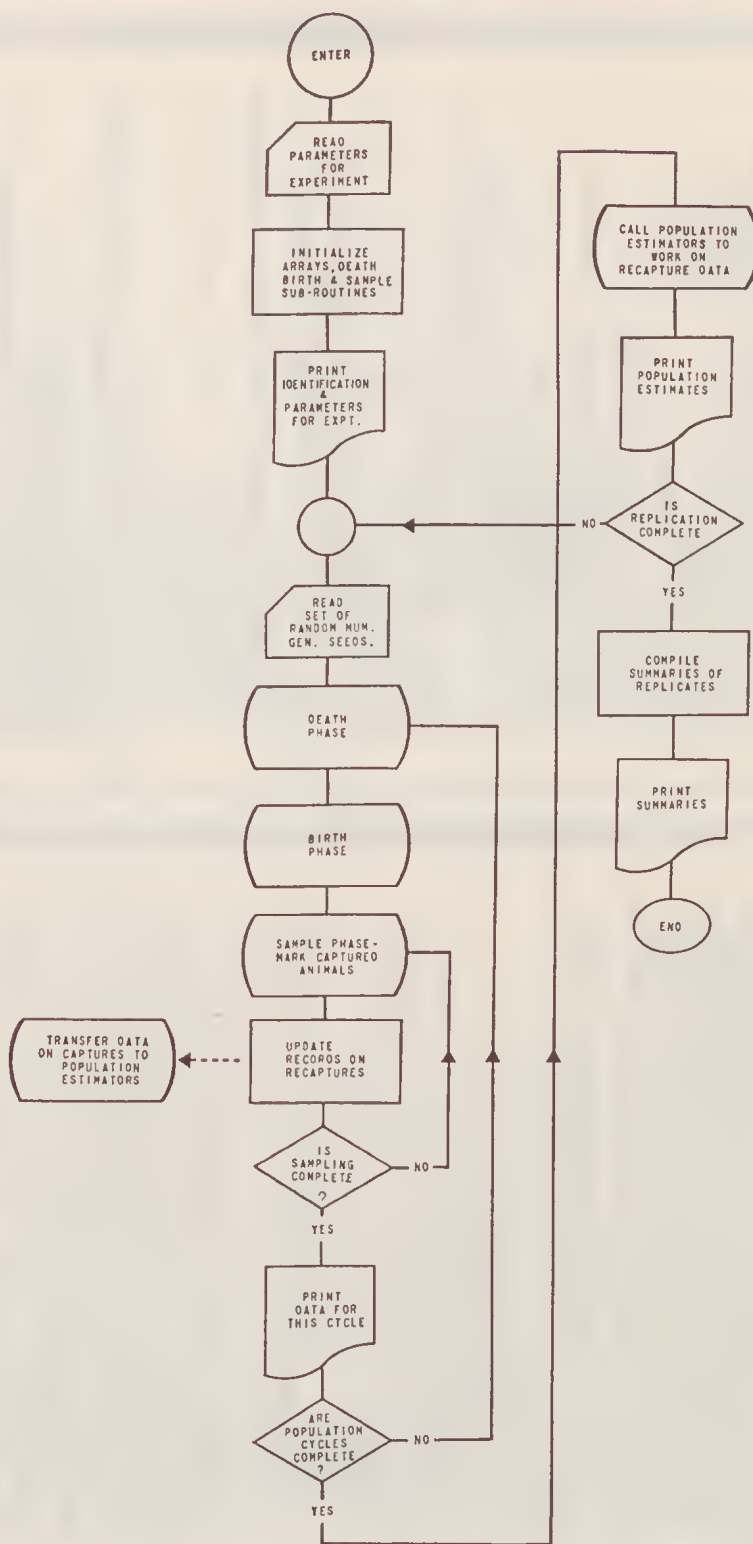


Fig. 16

FORTAN 4 LISTING OF PROGRAM 'SYNPOP'

12	CAPTURE/RELEASE OPTION	0 = RELEASES = CAPTURES (DEFAULT VALUE) 1 = RELEASES, 2 = CAPTURES
1A-20	PROBABILITY ANIMAL IS KILLED DURING HANDLING	
21-25	FIXED NUMBER PER SAMPLE (E.G. 100)	
26-30	ALLOWABLE VARIATION FOR SAMPLE E.G. .23	
31-35	FIXED PERCENTAGE PER SAMPLE E.G. .23	
36-40	ALLOWABLE VARIATION FOR SAMPLE E.G. .23	
41-45	OPTION - PRINT FULL INFO FOR EACH CYCLE	
46-50	OPTION - PRINT ANIMAL POP	
51-55	NO. OF REPLICATES	
56-60	2. BIRTH CARDS	
61-65	CARD 1	
66-70	CARD 2	
71-75	CARD 3	
76-80	CARD 4	
81-85	CARD 5	
86-90	CARD 6	
91-95	CARD 7	
96-100	CARD 8	
101-105	CARD 9	
106-110	CARD 10	
111-115	CARD 11	
116-120	CARD 12	
121-125	CARD 13	
126-130	CARD 14	
131-135	CARD 15	
136-140	CARD 16	
141-145	CARD 17	
146-150	CARD 18	
151-155	CARD 19	
156-160	CARD 20	
161-165	CARD 21	
166-170	CARD 22	
171-175	CARD 23	
176-180	CARD 24	
181-185	CARD 25	
186-190	CARD 26	
191-195	CARD 27	
196-200	CARD 28	
201-205	CARD 29	
206-210	CARD 30	
211-215	CARD 31	
216-220	CARD 32	
221-225	CARD 33	
226-230	CARD 34	
231-235	CARD 35	
236-240	CARD 36	
241-245	CARD 37	
246-250	CARD 38	
251-255	CARD 39	
256-260	CARD 40	
261-265	CARD 41	
266-270	CARD 42	
271-275	CARD 43	
276-280	CARD 44	
281-285	CARD 45	
286-290	CARD 46	
291-295	CARD 47	
296-300	CARD 48	
301-305	CARD 49	
306-310	CARD 50	
311-315	CARD 51	
316-320	CARD 52	
321-325	CARD 53	
326-330	CARD 54	
331-335	CARD 55	
336-340	CARD 56	
341-345	CARD 57	
346-350	CARD 58	
351-355	CARD 59	
356-360	CARD 60	
361-365	CARD 61	
366-370	CARD 62	
371-375	CARD 63	
376-380	CARD 64	
381-385	CARD 65	
386-390	CARD 66	
391-395	CARD 67	
396-400	CARD 68	
401-405	CARD 69	
406-410	CARD 70	
411-415	CARD 71	
416-420	CARD 72	
421-425	CARD 73	
426-430	CARD 74	
431-435	CARD 75	
436-440	CARD 76	
441-445	CARD 77	
446-450	CARD 78	
451-455	CARD 79	
456-460	CARD 80	
461-465	CARD 81	
466-470	CARD 82	
471-475	CARD 83	
476-480	CARD 84	
481-485	CARD 85	
486-490	CARD 86	
491-495	CARD 87	
496-500	CARD 88	
501-505	CARD 89	
506-510	CARD 90	
511-515	CARD 91	
516-520	CARD 92	
521-525	CARD 93	
526-530	CARD 94	
531-535	CARD 95	
536-540	CARD 96	
541-545	CARD 97	
546-550	CARD 98	
551-555	CARD 99	
556-560	CARD 100	
561-565	CARD 101	
566-570	CARD 102	
571-575	CARD 103	
576-580	CARD 104	
581-585	CARD 105	
586-590	CARD 106	
591-595	CARD 107	
596-600	CARD 108	
601-605	CARD 109	
606-610	CARD 110	
611-615	CARD 111	
616-620	CARD 112	
621-625	CARD 113	
626-630	CARD 114	
631-635	CARD 115	
636-640	CARD 116	
641-645	CARD 117	
646-650	CARD 118	
651-655	CARD 119	
656-660	CARD 120	
661-665	CARD 121	
666-670	CARD 122	

1	FORMAT STATEMENTS	123	C
1	FORMAT(16,3,12,1X,F5.3,3,2,15,2,5,0,3X,2(1,15))	124	C
2	FORMAT(2,5,0,1,2,20(1,3,3,1,17X,2,20(3,2))	125	C
3	FORMAT(1)	126	C
4	FORMAT(1)	127	C
5	FORMAT(1)	128	C
6	FORMAT(1)	129	C
7	FORMAT(1)	130	C
8	FORMAT(1)	131	C
9	FORMAT(1)	132	C
10	FORMAT(1)	133	C
11	FORMAT(1)	134	C
12	FORMAT(1)	135	C
13	FORMAT(1)	136	C
14	FORMAT(1)	137	C
15	FORMAT(1)	138	C
16	FORMAT(1)	139	C
17	FORMAT(1)	140	C
18	FORMAT(1)	141	C
19	FORMAT(1)	142	C
20	FORMAT(1)	143	C
21	FORMAT(1)	144	C
22	FORMAT(1)	145	C
23	FORMAT(1)	146	C
24	FORMAT(1)	147	C
25	FORMAT(1)	148	C
26	FORMAT(1)	149	C
27	FORMAT(1)	150	C
28	FORMAT(1)	151	C
29	FORMAT(1)	152	C
30	FORMAT(1)	153	C
31	FORMAT(1)	154	C
32	FORMAT(1)	155	C
33	FORMAT(1)	156	C
34	FORMAT(1)	157	C
35	FORMAT(1)	158	C
36	FORMAT(1)	159	C
37	FORMAT(1)	160	C
38	FORMAT(1)	161	C
39	FORMAT(1)	162	C
40	FORMAT(1)	163	C
41	FORMAT(1)	164	C
42	FORMAT(1)	165	C
43	FORMAT(1)	166	C
44	FORMAT(1)	167	C
45	FORMAT(1)	168	C
46	FORMAT(1)	169	C
47	FORMAT(1)	170	C
48	FORMAT(1)	171	C
49	FORMAT(1)	172	C
50	FORMAT(1)	173	C
51	FORMAT(1)	174	C
52	FORMAT(1)	175	C
53	FORMAT(1)	176	C
54	FORMAT(1)	177	C
55	FORMAT(1)	178	C
56	FORMAT(1)	179	C
57	FORMAT(1)	180	C
58	FORMAT(1)	181	C
59	FORMAT(1)	182	C
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62	FORMAT(1)	185	C
63	FORMAT(1)	186	C
64	FORMAT(1)	187	C
65	FORMAT(1)	188	C
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69	FORMAT(1)	192	C
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72	FORMAT(1)	195	C
73	FORMAT(1)	196	C
74	FORMAT(1)	197	C
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85	FORMAT(1)	208	C
86	FORMAT(1)	209	C
87	FORMAT(1)	210	C
88	FORMAT(1)	211	C
89	FORMAT(1)	212	C
90	FORMAT(1)	213	C
91	FORMAT(1)	214	C
92	FORMAT(1)	215	C
93	FORMAT(1)	216	C
94	FORMAT(1)	217	C
95	FORMAT(1)	218	C
96	FORMAT(1)	219	C
97	FORMAT(1)	220	C
98	FORMAT(1)	221	C
99	FORMAT(1)	222	C
100	FORMAT(1)	223	C
101	FORMAT(1)	224	C
102	FORMAT(1)	225	C
103	FORMAT(1)	226	C
104	FORMAT(1)	227	C
105	FORMAT(1)	228	C
106	FORMAT(1)	229	C
107	FORMAT(1)	230	C
108	FORMAT(1)	231	C
109	FORMAT(1)	232	C
110	FORMAT(1)	233	C
111	FORMAT(1)	234	C
112	FORMAT(1)	235	C
113	FORMAT(1)	236	C
114	FORMAT(1)	237	C
115	FORMAT(1)	238	C
116	FORMAT(1)	239	C
117	FORMAT(1)	240	C
118	FORMAT(1)	241	C
119	FORMAT(1)	242	C
120	FORMAT(1)	243	C
121	FORMAT(1)</		


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56 WRITE(LL,35) DENUAY,OFTE
57 GOTO 60
58 WRITE(LE,37)
59 CONTINUE
C
C GET INITIAL POPULATION ROWN
60 DO 1=1,SEED
61 POP(I)=99
C
C COMMFNC POPULATION CYCLES
62 DO 400 KK=1,NCYCL
63 CHECK IF POPULATION WITHIN BOUNDS = IE NOT, INCRFASF BOUND
64 IF(PUPSIZ*GT*MAXPOP) MAXPOP=PUPSIZ
65 ZFRO COUNTFNS
66 NKKLU=0
67 NPEL=0
68 NCAP=0
69 KMARK=0
70 NKSAB=0
71 LINCXK=0
72 NS=0
73 RT=0
74 POPNUM=PUPSIZ
75 MAXPUP=MAXPUP
C
76 PREPARE ALL PREVIOUSLY MARKED ANIMALS TO RECEIVE A NEW MARK
77 IF(KK*EQ*1)GOTO 397
78 IF(KK*EQ*1)MAXPOP
79 POP(I)=J=1,MAXPOP
80 POP(J)=99
81 IF(JUE*NE*99*AND*JUE*NE*0)POP(J)=POP(J)*10
82 CONTINUE
397 CONTINUE
C
C OBTAIN NUMBER OF DEATHS FOR THIS CYCLE
97 CALL DEATH(KK*POP*SIZ*NUOTH*LINO*PROTH*UTMHT*NOFU*OF*UOAY*OFRT*
1 NCYCL,IG,910)
C
C OBTAIN NUMBER OF BIRTHS FOR THIS PERIOD
98 CALL BIRTH(KK*POP*SIZ*NUOTH*NUOTH*NUOTH*NUOTH*NUOTH*NUOTH*NUOTH*
1 RT*TE*NCYCL*IRO*IN,920)
C
C KILL OFF PREVIOUS NUMBER OF ANIMALS
C
C IF(NUOTH*GT*POP*SIZ) GOTO 950
C IF(NUOTH*EQ*0) GOTO 175
C DO 170 I=1,NUOTH
100 NM=IFIX(RNUM(I)*MAXPOP*0.5)
C IF(NUM*GT*MAXPOP) NUM=MAXPOP
C IF(NUM*LT*1) NUM=1
C CHECK IF ANIMAL ALREADY DFAU
C IF(POP(NUM))100,100,140
C CHECK IF ANIMAL UNMARKED = IF SO KILL HIM
140 IF(POP(NUM)*99)150,150,150
C IF ANIMAL ALREADY MARKED, KEEP HIS RECORD IN "ALOKIL" AND TRFH
C KILL HIM
150 RT*KT+1
C ALOKIL(X)=POP(NUM)
160 POP(NUM)=0
C NOKU=NEAO*1
C POPSIZ=POP*SIZ-1
170 CONTINUE

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175 POP*DC=PUP*SIZ
C
C ENTER NINTH CYCLE
180 NM=NUMBTH
181 IF(NUMBTH*F*U*U)GOTO 270
182 DO 200 J=1,MAXPOP
183 IF(POP(J)) 200,180,200
184 POP(J)=99
185 POPSIZ=POP*SIZ+1
186 IF(NUMBTH*EQ*1) GOTO 270
187 NM=NUMBTH*F*U*U+1
188 NM=MAXPOP+1
189 MAXPOP=MAXPOP+NUMBTH
190 DO 260 J=MAX*MAXPOP
191 POP(J)=99
192 POPSIZ=POP*SIZ+1
193 CONTINUE
260 CONTINUE
270 CONTINUE
271 NNNSPL=PUP*SIZ
272 IRUPUP(KK)=PUP*SIZ
C
C URAN SAMPLES
273 CALL SAMPLECUMN*POP*SIZ*NSAMPL*LIMIT*PERSPL*VAR*IS,9900)
274 IF(NUM*LT*POP*SIZ)GOTO 270
275 WRITE(LE,942) NM,NM,POP*SIZ
276 NM=POP*SIZ
277 DO 340 J=1,NNN
278 SELECT LIVE ANIMAL
290 NM=IFIX(RNUM(I)*MAXPOP*0.5)
C IF(NUM*GT*MAXPOP)NUM=MAXPOP
C IF(NUM*LT*1)NUM=1
C CHECK IF THIS ANIMAL IS OFAO (=0) = IF SO, GET ANOTHER ANIMAL
320 IF(POP(NUM))290,290,330
C CHECK IF PREVIOUSLY MARKED
330 IF(POP(NUM)*99)340,335,340
C ANIMAL NOT MARKED
335 POP(NUM)=1
336 NCAP=NCAP+1
337 GOTO 355
C
C ANIMAL CARRIES A MARK
C
C IFST IF ANIMAL MARKED ALREADY IN THIS CYCLE
340 MARK*POP(NUM)
C MARK*MARK*-(MARK*10)*10)
C IF SO RETURN AND SELECT ANOTHER BEAST
350 IF(MARK*1)345,290,345
C IF NOT,CALL POPULATION COUNTERS
355 IF(CK*EQ*1) GOTO 350
C JK=POP(NUM)
C IF(CJK*10*(CJK*100)*10)EQ*1) LINCXK=LINCXK+1
C KSNAB=KSNAB+1
356 MARK*MARK*-(MARK*10)
357 CALL JOLLY(CJK,JMK)
358 CALL JOLLY(CJK,JMK)
359 IF NOT, MARK IT
360 CALL JOLLY(CJK,JMK)
361 POP(NUM)=POP(NUM)+1
362 NCAP=NCAP+1
363 CHECK IF ANIMAL KILLED IN MARKING
365 IF(CCR)360,360,360
366

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360 CONTINUE
  PRGRNUM(IIT)
  IF(PROB-PR370,370,360)
  C TRANSFER RECORD OF MARKED ANIMAL TO ARRAY "SNPLOC"
370 KS=KS+1
  SNPLOC(KS)=POP(NUM)
  POP(NUM)=0
  POPSIZ=POPSIZ+1
  HREF=NREL-1
380 CONTINUE
  WRITE(LP,39)IFLAG
  IFLAG=IFLAG+1
  C
  CALL SCHNAB(KK,MKSNAB,NCAP,NREL,NREPS,NRP)
  C
  C GATHER UP DATA FOR THIS CYCLE
  TOTCAP(KK)=NCAP
  TOTREL(KK)=NREL
  SCAP(KK)=TOTCAP(NCAP)
  SREL(KK)=TOTREL(NREL)
  TOTMK(KK)=LINCCK
  C
  C PRINT OUT RESULTS FOR THIS CYCLE
  IF(MK+EQ.0)GOTO 415
  WRITE(LP,40)KK
  WRITE(LP,41)MXPUP,NMXPUP,NOFAD,NPOPC,NNNBTH,NNNSPL
  WRITE(LP,42)MKSNAB,NREL,KS,KT
  IF(MKSNAB)GOTO 405,405,402
402 WRITE(LP,43)
  WRITE(LP,44)M*ARX(KK),K=1,MKSNAB)
405 IF(KS) GOTO 410,407
407 WRITE(LP,45)
  WRITE(LP,46)SMPLD(KK),K=1,KS)
410 IF(KT) GOTO 418,415
415 WRITE(LP,47)
  WRITE(LP,48)LDKIL(K),K=1,KT)
418 IF(MPR+EQ.0)GOTO 420
  WRITE(LP,49)
  WRITE(LP,50)POP(KK),K=1,MAXPOP)
420 KCYCL=KK
  C
  KOUNT=0
  DO 500 I=1,MAXPOP
    MARK=PUP(I)
    IF(MARK+EQ.99) KOUNT=KOUNT+1
500 CONTINUE
    MKANL=POPSIZ-KOUNT
    A=MKANL
    B=POPSIZ
    PFKMS=1/R*100.0
    WRITE(LP,51)KOUNT,MKANL,PFKMS
  C
  CALL LINCCKCYCL(TOTCAP,TOTREL,TOTMK,NREPS,NRP)
  CALL SNABR(KCYCL,NRP,NREPS)
  CALL BAIL2(KCYCL,NRP,NREPS)
  CALL JOLLY2(KCYCL,NRP,NREPS)
  CALL TRUVAL(KCYCL,NRP)
  IF(NRP+EQ.NHEPS)CALL TRUPRT(KCYCL,NREPS)
  GOTO 1000
427
  C

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A11 C IF(NRP.FG.1)CALL SNBSUM(NRPS,ARK)
A12 C IF (K-1)10,10,30
A13 C 10 UN 20 I=1,20
A14 C UN 15 J=1,9
A15 C 15 NAB(I,J)=0
A16 C UN 20 J=1,4
A17 C 20 ANS(I,J)=0.0
A18 C NAB(I,J)=K
A19 C NAB(I,J)=NREL
A20 C 30 NAB(K,1)=K
A21 C NAB(K,2)=NCAP
A22 C NAB(K,3)=NREL
A23 C NAB(K,4)=NAB(K-1,4)+NAB(K-1,3)+NAB(K-1,6)
A24 C NAB(K,5)=NAB(K-1,5)+NAB(K,2)+NAB(K,4)
A25 C NAB(K,6)=NAB(K-1,6)+NAB(K,5)
A26 C NAB(K,7)=NAB(K-1,7)+NAB(K,6)
A27 C NAB(K,8)=NAB(K,5)/(NAB(K,7)+1)
A28 C ANAB(K,5)
A29 C ANAB(K,8)
A30 C IF(A.E.0.0)GOTO 50
A31 C ANS(K,1)=SQRT((C+C/A)*(1+C+2.0/A))
A32 C ANS(K,2)=(NAB(K,8)-THUPP(K))/TRUPP(K)
A33 C CALL SUBSNB(K,C,AR,NCYCL)
A34 C 50 RETURN
A35 C
A36 C ENTRY SNARPP(N,NRP,NRPS)
A37 C WRITE(10,1)
A38 C UN 60 I=1,N
A39 C CONTINUE
A40 C 1 FORMAT(1H0,10,10,20,POPULATION ESTIMATES - SCHNABFL POPULATION,
A41 C 2,PERFIO NUM,10,20, ON LINCOLN INTER,10,20, BIAS,10,
A42 C 3,20X, NUM, NUM, NUM, ESTD. SE,
A43 C 4, CAPTO. RELU. RCAPS MARKS POPLN,10,
A44 C 5,FORMAT(2X,10,5,12(2X,F8.4))
A45 C IF(NRP.1)NRP=0
A46 C CALL SNBTT(NRPS)
A47 C K=CTC(NRPS)
A48 C CALL PRINT(NRP,NRPS,K,42)
A49 C RETURN
A50 C
A51 C SUBROUTINE BAILY(NRP,NRPS)
A52 C *****
A53 C SUBROUTINE BAILY ESTIMATES ANIMAL POPULATION SIZE FROM MARK
A54 C RECAPTURE DATA BY BAILY'S TRIPLE-CATCH METHOD.
A55 C OFF. BAILY, N.J.J. 1942. IMPROVEMENTS IN THE INTERPRETATION OF
A56 C RECAPTURE DATA. J. AM. ECOL. 21, 120-7
A57 C
A58 C USE = CALL BAILY(NQ)
A59 C CALL BAILY(K,NUM)
A60 C CALL BAILY
A61 C COMMON TC,TR,TRUPP, /COMMON/AR,DC
A62 C WHERE ND = NUMBER OF TRAPPING DAYS
A63 C K = ORDER NUMBER OF ANY TRAPPING DAY
A64 C NUM = MARK CODE OF AN ANIMAL, IN THE FORM 11010,
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A67 C
A68 C
A69 C
A70 C
A71 C
A72 C
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A77 C
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      240 Z(J1)=Z(J1)+TEMP(I)
      250 CONTINUE
C.
C. CALCULATE POPULATION STATISTICS
C. ANS(I) = PROPORTION OF MARKED ANIMALS (ALPHA)
C. (2) = NO. OF MARKED ANIMALS (M)
C. (3) = POPULATION ESTIMATE (P)
C. (4) = PROBABILITY OF SURVIVAL (PHI)
C. (5) = NO. OF NEW ANIMALS JOINING POPULATION (B)
C. (6) = STANDARD ERROR OF P
C. (7) = STANDARD ERROR PHI
C. (8) = BIAS OF ESTIMATE
C.
      300 I=2,NC
      IF(TEMP(I)) 300,300,252
      252 ANS(I,1)=TEMP(I)/TOTCAP(I)
      254 IF(SRECAP(I))Z(I)=300,300,260
      260 ANS(I,2)=Z(I)*((TOTREL(I)+1)/(SRECAP(I)+1))*TEMP(I)+1
      ANS(I,3)=(ANS(I,2)-TRUPOP(I))/TRUPOP(I)
      300 CONTINUE
      300 I=I+1
      310 I=I+1
      315 CONTINUE
      320 I=2,NB
      320 ANS(I,5)=ANS(I,3)-(ANS(I,4)*ANS(I,3)-TOTCAP(I)+TOTREL(I)))
C.
C. HFAOINGS
C. WRITE(CLP,20)
C. WRITE(CLP,25)
C. WRITE(CLP,30)
C. WRITE(CLP,35)
C. WRITE(CLP,40)
C. WRITE(CLP,45)
C.
C. UINPUT RESULTS
      330 I=1,N0
      330 WRITE(CLP,50) I, (ANS(I,1),J=1,8)
      330 CONTINUE
      330 IF(CNRP.LT.NREPS)RETURN
      330 CALL JOLIT(CNRFPS)
      330 CALL PRINT(CNRP,NREPS,L,AR)
      330 RETURN
      330 ENO

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STUDIES ON AUSTRALIAN CAINOZOIC BRACHIOPODS

1. THE LOOP DEVELOPMENT OF *FRENULINA*
SANGUINOLENTA (GMELIN 1790)

By JOYCE R. RICHARDSON*

ABSTRACT: A description is given of the growth stages of the loop of *Frenulina sanguinolenta* from Australian waters which supplements the four stages described by Deslongchamps from Tahiti in 1884. Early growth stages are characterized by the presence of septal flanges which, in later development, form projections of the transverse band. Later growth stages show that, with regard to loop structure, the affinities of *F. sanguinolenta* lie with *Kingena* and *Aldingia*.

INTRODUCTION

The familial classification of the Terebratulacea is based on the developmental and adult patterns of the loop. The subfamilies of the Dallinidae (of which *Frenulina* is at present a member) are differentiated on the loop patterns exhibited within a range of stages defined as dallinid (Elliott 1953). Since Elliott's review the loop development of some members of the Dallinidae, *Macandrevia cranium* (Müller), *Terebratalia transversa* (Sowerby) and *Fallax dalliniformis* Atkins, has been studied carefully by Atkins (1959a, 1959b, 1960). No two of these dallinid genotypes show identical patterns of loop development, Atkins (1959b) suggesting, for example, that *T. transversa* may need to be placed in a separate subfamily or family.

The earliest stages of development are of particular interest since they demonstrate most of the diagnostic features upon which loop classifications are based i.e. the origin of the descending branches, the development of a hood or a ring upon the septum and whether or not additional structures, the flanges, arise on the septum. In 1884 Deslongchamps described stages in the loop development of *Terebratula* (in plates ascribed to *Terebratella*) *sanguinea* (Chemnitz) = *Frenulina sanguinolenta* (Gmelin) from Tahiti. Deslongchamps figured the loops of four specimens 4 mm, 5 mm, 8 mm and 10 mm in total shell length. A large collection of young specimens of *F. sanguinolenta* from Masthead Island, Queensland, was available to the author from the Invertebrate De-

partment, National Museum of Victoria. These included all growth stages of structures giving rise to the loop from the first appearance of the median septum at a shell length of 1.1 mm. The following account of the loop development of *F. sanguinolenta* includes a comparison with the stages described by Deslongchamps.

TERMINOLOGY

The terminology used to describe the growth stages of the loop and parts of the adult loop is in need of revision for the whole phylum. Until this is done it has been decided, following Atkins (1959a), not to use the terminology employed by palaeontologists to describe the growth stages of the loop i.e. with names derived from the adult genus showing a particular pattern. The growth stages of the loop are of sufficient complexity without giving them names which may need to be altered with any classificatory change. For example in the *Treatise* (1965) the Dallinidae (diagnosis by Elliott and Hatai) is typified in its loop development by a precampagiform stage; whereas the same stage in Hatai's diagnosis (loc. cit.) of the dallinid subfamily Frenulininae is termed preismeniform, a stage name which Elliott in 1947 had declared to be inaccurate on taxonomic grounds. Concerning the adult loop of *F. sanguinolenta*, two structures defined in the *Treatise* as precampagiform flanges (p.H150) and laqueiform connecting bands (p.H142) are referred to in more detail in the discussion. The existence of precampagiform flanges or of campagiform flanges has not been demonstrated in any

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species of *Campages* and so these structures are termed here septal flanges. The laqueiform connecting bands are referred to as vertical connecting bands.

GROWTH STAGES OF THE LOOP

The youngest developmental stage at a length of 1.1 mm (all lengths cited are of the ventral valve i.e. the maximum shell length) displays a low median septum, triangular in outline, with a thickened crest or free border (Fig. 1A). The septum is situated anterior to the mid-line of the valve, but in later growth stages comes to occupy the mid-segment of the valve. The septum itself develops into a high, plate-like structure with a lateral outline roughly the shape of a parallelogram, its ventral border forming the crest of the septum (Fig. 1B). Midway along the length of the posterior border is a thickened area from which spinous projections extend laterally. At this growth stage (1.4 mm) socket ridges are defined as low, subarcuate ridges which delimit the postero-lateral areas of the valve floor as sockets. The posterior border of the valve is slightly thickened.

In succeeding growth stages the anterior border of the septum is eroded, the spinous projections on its posterior border expand to form lamellar plates (= flanges of Atkins 1959b) and a low ridge develops which extends from the area of the developing cardinalia to the posterior limit of the septum (Fig. 2A, B). By the time a shell length of 2.2 mm has been reached the lateral plates or flanges form projections from the posterior border of a hood which appears as a flared extension of both the crest of the septum and of the flanges. The socket ridges are now higher, the

area of the cardinal process is defined and slight thickenings extending medio-laterally from the socket ridges mark the anterior borders of the hinge plates. Crura and crural processes extend from areas at the bases of the socket ridges. This growth stage is similar to that described by Atkins (1959b) for *T. transversa* at a shell length of 3.4 mm. Both species display a hood with lateral expansions, defined crura and crural processes and no indication of descending branch attachments to the septum. The only apparent difference is that the crest of the septum is thicker in *T. transversa*. There are also similarities to Elliott's (1947) description of the earliest stage (2.5 mm) observed of *Genmarcula aurea* (Sowerby) in which the flanges, in roofing a grooved septum, form a tunnel over the posterior crest of the septum.

In shells between 2.6 and 3 mm in length the attachments of the descending branches to the septum appear as triangular lamellar plates with oblique lines of insertion running parallel with the hood attachments to the septum. At this growth stage (Fig. 3A, B) there is some variation in different specimens in the extent of erosion of the anterior border of the septum, as a result of which the position of the descending branch attachments varies relative to the anterior border. There is also variation in the shape, thickness, size and position of the hood; it may be confined to the posterior border or envelop part of the latter together with a section of the crest of the septum. This stage may be compared with that of *T. transversa*

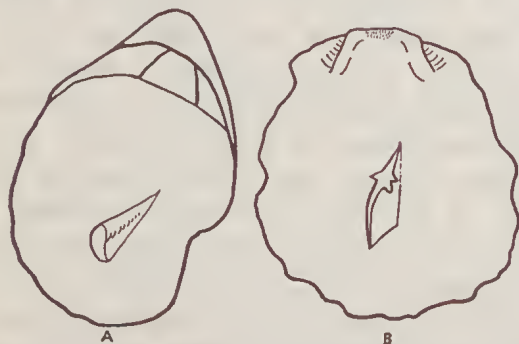


FIG. 1—*Frenulina sanguinolenta*. Oblique side views of interiors of dorsal valves. A, specimen of shell length 1.1 mm with early septum, hypotype NMV H175; B, septum showing spinous projections in specimen with a total shell length of 1.4 mm, hypotype NMV H176. All figures have been drawn with the aid of a camera lucida.

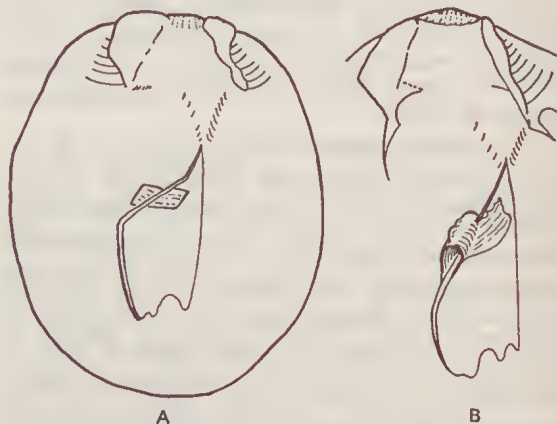


FIG. 2—*Frenulina sanguinolenta*. Oblique side views of interiors of dorsal valves. A, specimen 1.8 mm in length displaying septal flanges, hypotype NMV H177; B, specimen 2.2 mm in length displaying septal hood and one flange, flange on left hand side broken as are the socket ridges on the right side of both specimens. The dotted line indicates the extent to which the developing hinge plates are raised off the valve floor, hypotype NMV H178.

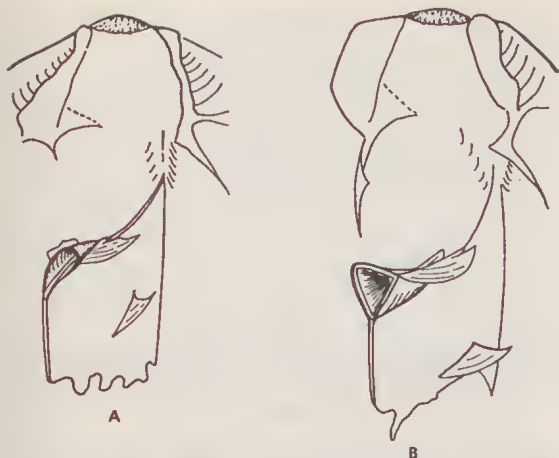


FIG. 3—*Frenulina sanguinolenta*. Oblique side views of dorsal valve interiors each showing the median septum with descending branch attachments in addition to the hood and flanges. A, 2.6 mm in length, both socket ridges broken, hypotype NMV H179; B, 3.0 mm in length, socket ridge on right side broken, hypotype NMV H180.

(Atkins 1959b, Fig. 6) at a shell length of 4.6 mm.

The next growth stage (3.8 mm, Fig. 4A) shows complete descending branches with long lines of attachment to the septum. The hood with its flanges has been converted into a broad lamellar ring with postero-lateral horns. This is a stage similar to that described by Atkins for *T. transversa* at a shell length of 5.2 mm (1959b, Fig. 7). Deslongchamps figures a specimen of *F. sanguinolenta* with complete descending branches and a tiny hood on the crest of the septum at a shell length of 4 mm (1884, Pl. 5, fig. 1). The next growth stage he describes at 5 mm (1884, Pl. 5, fig. 2) is more similar to the 3.8 mm stage described here i.e. with a ring (derived from the hood by the resorption of its posterior end) arching over the crest of the septum.

An individual with a shell length of 4.2 mm shows the anterior fusion of the attachments of the ring and of the descending branches (Fig. 4B). In this individual the fusion has occurred while the septum extends beyond the anterior and ventral limits of these attachments i.e. the septum forms a partition against which the fused attachments lie on either side. In other specimens observed the anterior fusion of the attachments occurs almost simultaneously with the complete anterior resorption of the septum so that it is difficult to differentiate between parts of the septum and of the fused attachments. These differences in the timing of resorption and fusion in this area at this stage may be influenced by the extent to which

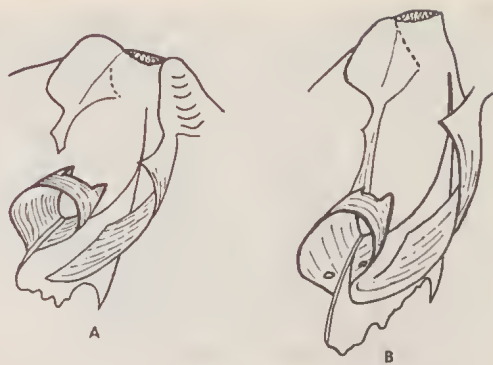


FIG. 4—*Frenulina sanguinolenta*. Oblique side views of dorsal interiors. A, 3.8 mm in length, descending branches complete and a ring with postero-lateral horns replacing the earlier hood and flanges, hypotype NMV H181; B, 4.2 mm in length with anterior fusion of the attachments to the septum of the ring and the descending branches and with small lacunae perforating the bands of the ring, hypotype NMV H182.

the ring occupies the crest of the septum. As noted above, the early hood varies in its position on the septum. In addition the descending branch attachments vary in the distance they lie from the anterior border of the septum. Thus both the hood and the early descending branch attachments may extend to the anterior limits of the septum in which case resorption of the septum and fusion of the attachments apparently occur simultaneously. If, on the other hand, the attachments of the descending branches and the hood or the ring lie posterior to the anterior border of the septum then the process of fusion of the attachments may be seen as distinct from septal resorption. Until this stage was observed it sometimes appeared as if a component derived from the septum contributed to the regions of fusion of the ring and the descending branches.

At a growth stage of 4.7 mm (Fig. 5A, B) the results of the progressive resorption of the crest and the anterior border of the septum are seen i.e. the fused attachments of the ring and the descending branches are now separated anteriorly. Posteriorly these lines of attachment are not fused and are still separately attached to the septum. At this stage the anterior (and dorsal) segments of the ring are perforated by lacunae apparent as small perforations in the previous growth stage. The adult loop is becoming apparent as a result of the enlargement of these lacunae and of the progressive anterior resorption of the septum combined with the fusion of descending branch and ring attachments. The posterior and ventral segment of the ring forms the transverse band from which projects the postero-lateral

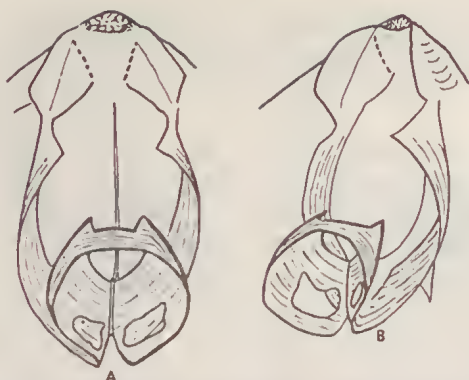


FIG. 5—*Frenulina sanguinolenta*. Ventral view (A) and oblique side view (B) of a specimen of shell length 4.7 mm showing the anterior separation of the fused attachments (of the ring and descending branches) and lacunae perforating the anterior and dorsal segments of the ring, hypotype NMV H183.

horns. Posterior to the lacunae the dorsal segments of the ring extend from the transverse band to the septum and represent the future frenuliform or vertical connecting bands. Anterior to the lacunae the anterior and lateral segments of the ring form the ascending branches. The posterior areas of attachment of the descending branches to the septum represent the future lateral connecting bands. This stage is similar to that described by Deslongchamps at a shell length of 8 mm (1884, Pl. 5, fig. 3) as the beginning of the megerliform stage: 'Non-seulement nous y retrouvons, comme dans l'état mégerliforme de la *t. cranium*, la lamelle externe *e*, la lamelle interne *i* et les 2 lamelles accessoires, qui déterminent avec le pont, l'espace triangulaire caractéristique de l'état mégerliforme; mais encore nous constatons, que la très-large lamelle représentant la partie médiane, en forme de pont, est reliée aux branches courantes par un petit processus quadrangulaire *a*, qui se rencontre aussi dans l'appareil adulte du genre *Laqueus*' (p. 187). From this account it is difficult to determine how the 'lamelles accessoires' and the 'petit processus quadrangulaire *a*' are related to each other. In his figures of *F. sanguinolenta* (Fig. 6 this paper) the 'lamelles accessoires' are not labelled and the labels for 'processus *a*' are directed to areas where the postero-lateral horns (not described in earlier growth stages of this species by Deslongchamps) and the vertical connecting bands (derived from the dorsal segments of the ring) are in juxtaposition. Undoubtedly Deslongchamps in relating 'processus *a*' with the bands seen in *Laqueus* is referring to the adult vertical connecting bands but their early relationship to other segments of the loop is not clear.

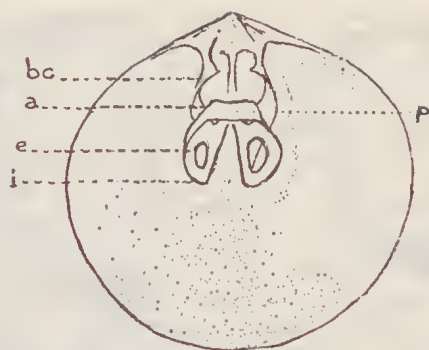


FIG. 6—*Frenulina sanguinolenta*. Photographic copy of Deslongchamps' figure of an 8 mm growth stage (1884, Pl. 5, fig. 3).

The variable character of earlier growth stages noted above is apparent also in different specimens at later growth stages. A comparison of Fig. 5 and of Pl. 4, fig. 1-3 shows differences in the diameter of the ring, in the width of its bands and in the length of the posterior segments of the descending branches relative to the total loop length. The specimen represented in Pl. 4, fig. 1-3, although at a relatively more advanced growth stage than that in Fig. 5A, B, displays a shorter, more compact loop, earlier growth stages of which must have displayed a ring of smaller diameter than that seen in the specimen in Fig. 5. As a result of this factor the vertical connecting bands (the dorsal segments of the ring) occupy a more extensive area posteriorly than they do in the specimen in Fig. 5.

The adult loop pattern (Pl. 4) is achieved as a result of the vertical connecting bands i.e. the dorsal segments of the ring changing their position relative to the septum. Two processes are involved: the reduction in width of the connecting bands, together with growth proceeding medial to these segments so that their lines of attachment are carried, with the attachments of the descending branches, away from the septum. As a result of these growth processes the ventral attachments of the vertical connecting bands remain fused to the transverse band but their dorsal attachments shift from the septum to the areas of union of the descending branches and the lateral connecting bands. The lateral connecting bands represent the remaining attachments of the descending branches to the septum.

DISCUSSION

The main features of the loop development of *F. sanguinolenta* are that the descending branches arise from both the crura and the septum; septal flanges precede the development of a hood, these combined structures being transformed into a ring

with posterior horns; lacunae in the anterior segments of the ring delimit ascending branches anteriorly and vertical connecting bands posteriorly. The adult loop of *F. sanguinolenta* consists of descending and ascending branches, a transverse band and two pairs of connecting bands, the lateral connecting bands running from the septum to the descending branches and the vertical connecting bands running from the transverse band to the lines of union of the descending branches and the lateral connecting bands. One feature which should be emphasized is the variation noted at various stages of loop development in the shape, size and position of the hood (and later the ring), in the position of descending branch attachments and in the fusion of descending branch and ring attachments relative to the extent of the septum.

As described above the vertical connecting bands in the adult occupy a different position from that in the penultimate growth stage. When first defined they run from the median septum to the outer borders of the transverse band. In their definitive adult position they extend from the descending branches to the transverse band. These bands have been referred to by a variety of terms as frenuliniform, laqueiform or posterior connecting bands. The desirability of using morphological terms instead of a terminology derived from a variety of genera is referred to above and since the term posterior connecting band could apply equally meaningfully to either set of bands it is proposed that they be referred to as *vertical connecting bands*. In both positions they occupy these connecting bands are vertical to all other parts of the loop. It is also proposed that they be differentiated according to the position they occupy, that the bands extending from the septum to the transverse band be termed the *medio-vertical bands* and that the bands between the transverse band and the descending branches be termed the *latero-vertical connecting bands*.

Although the general pattern and sequence of events is similar, there are some discrepancies in the accounts of the development of *F. sanguinolenta* given above and that of Deslongchamps. In the first place Deslongchamps does not describe the septal plates or flanges which become, in the adult, postero-lateral horns on the transverse band. Secondly there is a marked difference in the shell size of similar growth stages in the two accounts e.g. at a length of 5 mm most individuals examined by the author display the adult loop form while in a specimen of this length figured by Deslongchamps the septal structures are not fused and are more comparable with the 3.5 mm stage described above. In view of these differences it is pertinent to question whether we are dealing

with the same species. Adult specimens from Masthead Island agree in diagnostic features with material collected from fourteen different stations of the Sulu Archipelago which extends between Mindanao (the type locality of *F. sanguinolenta*) and North Borneo. In addition comparison has been made with material collected from a wide geographical area, from Hawaii, Tahiti, the Moluccas and Australia and the examination of this material confirms Cooper's statement (1957) that *F. sanguinolenta* is one of the most widespread modern brachiopods. Differences in the mean size of populations may account for the difference in growth stage sizes, although Deslongchamps is inaccurate in his transpositions of Friele's (1877) figures of *Macandrevia cranium* in the same paper. The presence of flanges in the material examined here and their absence in that of Deslongchamps could be due to the fact that Deslongchamps did not examine the very early stages in which they are so clearly apparent. Figures of the adult loop of *F. sanguinolenta* by Reeve (1862), Thomson (1927) and Hatai (1940) all show a transverse band with posterior horns.

Septal flanges have been described in the development of other species. As noted by Atkins (1959b) they occur in the development of *Terebratalia transversa* and of *Dallinella obsoleta* (Beceher) but are not retained as distinct structures on the transverse band of the loop. Other factors in the development of *T. transversa* and *D. obsoleta* also differentiate these species from *F. sanguinolenta* e.g. the absence of vertical connecting bands at any developmental stage. Elliott (1947) described flanges in *Gemmarcula aurea* (and Cooper 1955, for *G. arizonensis*) in both the developmental stages and in the adult loop where they appear as horns projecting from the transverse band. On the basis of the presence of flanges in both developmental stages and in the adult loop of *G. aurea*, Elliott created the new sub-family Gemmarculinae. There are a number of features characteristic of *F. sanguinolenta* which make one hesitate to refer it to the Gemmarculinae. The general pattern of loop development is similar although *Gemmarcula* is characterized by an early septum with a pronounced median groove, by the relatively early fusion of hood and descending branch attachments and by an adult loop with only one pair of connecting bands (the lateral bands) retained.

It seems that the presence of septal flanges does not necessarily indicate a close relationship between genera although a much more comprehensive study is required before any comments are of much value. This is also the case when considering the significance of the origin of the descending

branches and of the development of a hood or a ring on the early septum. In *F. sanguinolenta* the descending branches arise from both the crura and the septum. The double origin of the descending branches has been described for *Terebratalia transversa* by Atkins (1959b), *Terebratella dorsata* (Gmelin) by Fischer and Oehlert (1892) and for *Waltonia inconspicua* (Sowerby) by Thomson (1915). In the only other species, *Macandrevia cranium*, in which early growth stages before the completion of the descending branches are described, the descending branches arise from the crura alone. The early septum of *F. sanguinolenta* bears a hood which by the resorption of its posterior end becomes converted into a ring, a sequence apparent in other species derived from a number of different families.

The most striking resemblance to the loop structure of *F. sanguinolenta* occurs in the Australian Cainozoic genera *Aldingia* and a related new genus, and in the widely distributed Mesozoic genus *Kingena*. Adult examples of these genera display a loop identical in pattern with the penultimate growth stage of *Frenulina*, that is with vertical connecting bands in their medial position. The adult loops differ only in the relative widths of the different bands which make up the loop. The structure of the loop in these genera is discussed, with other morphological features, in the following paper (Proc. R. Soc. Vict. 86, Art. 11) in which *Frenulina* is transferred to the family Laqueidae.

ACKNOWLEDGMENTS

I wish to thank the Director and Staff of the National Museum of Victoria for providing the facilities to work with the Collections in their care. Dr. Barry Wilson of the Western Australian Museum supplied specimens from the Sulu Archipelago, the Moluccas and Tahiti. Mr. Frank Guy of the Royal Melbourne Institute of Technology took the photographs, the cost of which was cov-

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EXPLANATION OF PLATE 4

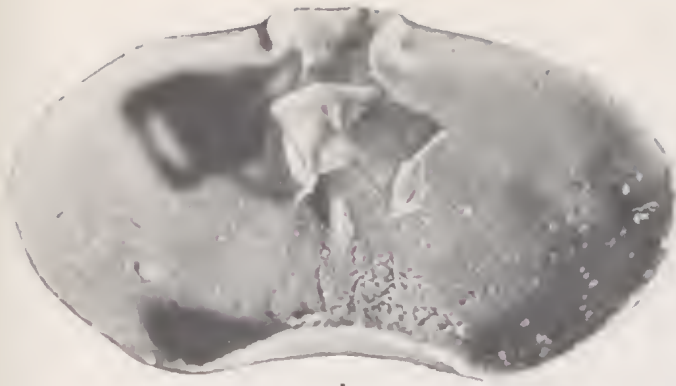
Three specimens of *Frenulina sanguinolenta* which show the change in position and extent of the vertical connecting bands in youth and maturity. In Fig. 1-3 the medial sections of the bands run between the transverse band and the septum, in Fig. 5-7 they extend from the transverse band to the descending branches. Fig. 4 shows the loop in an older adult specimen in which the vertical bands are seen as thin struts linking the transverse band and the areas of union of the descending branches and the lateral connecting bands.

FIG. 1-3—*Frenulina sanguinolenta*. Anterior, lateral and dorsal views of the dorsal interior of a specimen 8.0 mm in length, hypotype NMV H184, $\times 12$.

FIG. 4—*Frenulina sanguinolenta*. Anterior view of a dorsal interior of a specimen 11.5 mm in length, hypotype NMV H185, $\times 12$.

FIG. 5-7—*Frenulina sanguinolenta*. Anterior, lateral and dorsal views of the dorsal interior of a specimen 9.5 mm in length, hypotype NMV H186, $\times 8$.

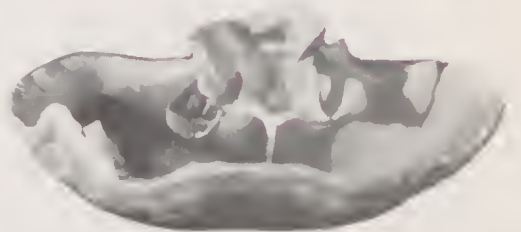
All specimens coated in magnesium oxide.



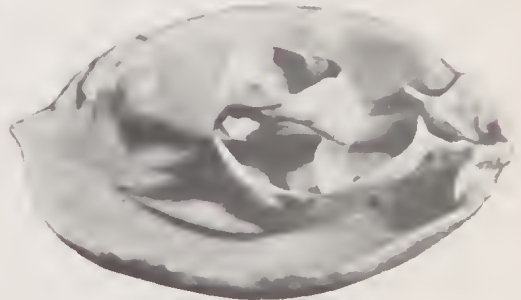
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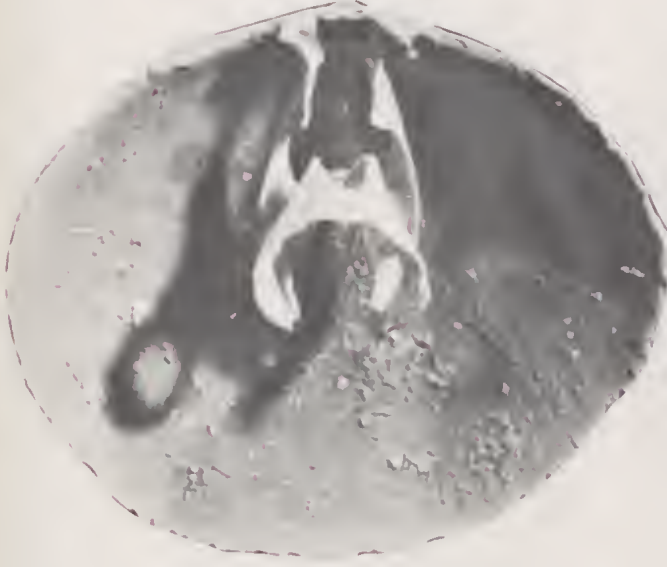
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STUDIES ON AUSTRALIAN CAINOZOIC BRACHIOPODS

2. THE FAMILY LAQUEIDAE (TEREBRATELLIDAE)

By JOYCE R. RICHARDSON*

ABSTRACT: The genera *Frenulina* and *Aldingia* are reviewed and a new genus *Paral dingia* described. The presence of dental plates and similarities in loop structure and cardinalia indicate that these genera are related to *Kingena* and to *Laqueus*. Since it holds precedence over the Kingenidae and the Frenulininae, all these genera are referred to the family Laqueidae.

INTRODUCTION

As a result of a study of the loop development of *Frenulina sanguinolenta* (Gmelin) and of the attribution of the Mioene species *Terebratella pumila* Tate to *Frenulina* a morphological pattern is apparent which indicates relationship with *Aldingia*, with *Kingena* and with *Laqueus*. Similarities in both the loop and cardinalia thus embrace genera at present distributed between four different families, the Dallinidae (*Frenulina*), Kingenidae (*Kingena*), Kraussinidae (*Aldingia*) and Laqueidae (*Laqueus*). *Aldingia* has been assigned incorrectly to the Kraussinidae but it is considered that the families Kingenidae and Laqueidae and the subfamily Frenulininae are synonymous. Therefore it is proposed that *Aldingia*, *Frenulina*, *Kingena*, *Laqueus* together with related genera be placed in the Laqueidae. Their familial position will be discussed in greater detail in a subsequent paper on terebratellacean loop development.

Family LAQUEIDAE THOMSON 1927

Owen (1970) proposed the separation of three Mesozoic genera, *Kingena*, *Zittelina*, *Belothyris*, from the main family Dallinidae. He suggested that structures of the loop in these genera 'the double attachment of brachial branches to septum and the expanded transverse band' (p. 49) warranted the elevation of Elliott's Kingeninae to family status. On this basis *Aldingia* and *Paral dingia* gen. nov. should be included in the Kingenidae: both possess a loop with two pairs of connecting bands attached to the septum and transverse bands with postero-lateral expansions. In addition these genera, like *Kingena*, display dental plates and a hinge platform with a posterior striated or roughened

area in place of the usual cardinal process. A particularly close resemblance is apparent between *Kingena mesembrina* (Etheridge) from Upper Cretaceous beds of Western Australia and *Paral dingia woodsii* (Tate) from Lower Mioene beds of Tasmania (Pl. 6, fig. 1-6).

From the accompanying study of the loop development of *Frenulina sanguinolenta* it may be seen that the penultimate growth stage of this species is the same pattern as that observed in adult specimens of *Kingena* (Pl. 6, fig. 1-3), *Aldingia* (Pl. 5, fig. 11-12) and *Paral dingia* (Pl. 6, fig. 4-6). In all these genera the loop displays two pairs of connecting bands, the lateral and the vertical. The vertical connecting bands run from the septum to the transverse band and are defined as medio-vertical connecting bands in the accompanying paper on the loop development of *F. sanguinolenta*. In *Kingena*, *Aldingia* and *Paral dingia* these bands are reduced in width in such a manner that they retain their connection with the median septum. In *F. sanguinolenta*, on the other hand, the reduction in width of the vertical connecting bands occurs simultaneously with their change in position. It is suggested that these differences may be accounted for by the differential erosion of the free borders of the vertical connecting bands; in *Kingena* and *Aldingia* there is greater resorption laterally than medially, the reverse being the case in *F. sanguinolenta*. In adult *F. sanguinolenta* these bands retain their ventral connection with the transverse band but their dorsal attachments lose their connection with the septum and lie across the lines of union of the lateral connecting bands and the descending branches. In this position the bands are defined as latero-vertical connecting bands which are present, with

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the lateral connecting bands, in the adult loop of *Laqueus* which differs from that of *F. sanguinolenta* only in possessing thinner bands.

The penultimate stage of the loop of *Frenulina sanguinolenta* had not been described in the only previous account of its development, that of Deslongchamps (1884). A study of the loop development of *Laqueus californianus* (Koch) by Konjoukova (1957) also omits the growth stages between the first appearance of the lacunae in the ring and the definitive adult pattern. Elliott (1953) however comments: 'Young adult *Frenulina sanguinolenta* illustrate how closely this process is to laqueiniform development. In this way the distinctive kingeniform loop was produced, with connecting bands from descending branches to septum' (p. 267). Owen (1970) has also noted that the adult loop of *Waconella* is the same as *Laqueus* and that young adult examples of *Waconella* display the adult loop pattern of *Frenulina* and claims that 'the Recent genera *Frenulina* and *Laqueus* have a similar loop development to that of *Kingena* and *Zittelina*' (p. 44).

Hence the adult loop structure of *Kingena*, *Belothyris*, *Zittelina*, *Aldingia* and *Paral dingia* is seen in a late growth stage of *F. sanguinolenta* whose adult pattern is characteristic of *Laqueus* and *Waconella*. With respect to cardinalia pattern all these genera except *Frenulina* display a hinge platform formed by the fusion of socket ridges, crural bases and hinge plates; no separate cardinal process is present. *F. sanguinolenta* is characterized by discrete inner hinge plates with free anterior and medial borders and a small transverse cardinal process. These apparently disparate patterns of cardinalia are linked by variants of *Frenulina pumila* (Tate). The adult loop of *F. pumila* is identical with that of *F. sanguinolenta* and the cardinalia pattern is common to some members of both species. The only method by which they may be separated is that they display different ranges of variation in external features (see this paper p. 119) and internally in the disposition of the hinge plates. The normal condition of the hinge plates in *F. sanguinolenta* is described above and there is little variation from this norm. On the other hand *F. pumila* shows considerable variation in the disposition of the hinge plates. They may be discrete as in *F. sanguinolenta*, they may be fused medially thus presenting the appearance of an excavate shelf, or their medial borders may fuse with the valve floor on either side of the median septum. All variants between these three main patterns are available. In displaying a wide range of variability in hinge plate pattern *F. pumila* provides links with other genera. Those specimens of *F. pumila*

in which the hinge plates are fused medially to form an excavate shelf bear a marked similarity to members of *Paral dingia*, particularly to *P. woodsii*. In neither species does the anterior border of the hinge plates fuse with the underlying septum (although fusion may occur near the posterior limits of each structure), a feature unique to these two species. In *F. pumila* a small cardinal process is present, in *P. woodsii* only its posterior surface is apparent as a striated area of the hinge platform. If one compares the illustrations of *Frenulina pumila* and *Paral dingia woodsii* in Pl. 5, fig. 7 and Pl. 6, fig. 4 it is not difficult to visualize how a small cardinal process could be incorporated in the hinge platform or alternatively how an area specialized for muscle attachment could be elevated by thickening from the hinge platform surface. A pattern similar to that of *P. woodsii* is evident in the cardinalia of *Laqueus* and *Kingena*, neither genera displaying a separate cardinal process. In *Kingena* the hinge plates and associated structures are free of the valve floor anteriorly but posteriorly are fused with the floor as a result of secondary thickening in the area; in *Laqueus* the hinge plates are excavate for their full length and are fused anteriorly on top of the septum. Thus from the variations exhibited by *Frenulina pumila* it may be seen how a relationship exists between the cardinalia patterns of *Frenulina*, *Paral dingia*, *Kingena* and *Laqueus*.

In brief then, the genera discussed above display two loop patterns both of which are seen in the ontogeny of one of these genera *Frenulina*. *Frenulina* also provides, in the variants of one of its species, the two patterns of cardinalia which may be associated with either loop pattern. Thus these genera appear to show random variation in two loop and two cardinalia patterns. All these genera possess dental plates and display rectimarginate to sulcate folding and it is felt that their separation into four different families cannot be justified. Therefore it is recommended that the Laqueidae includes *Aldingia*, *Paral dingia*, all members of the Kingenidae attributed to this family by Owen (1970) and, from the subfamily Frenulininae, *Frenulina* and *Jolonica*. The remaining member of the Frenulininae, *Kamoica*, is not well-documented; the loop is unknown and Hatai (1940) states that the cardinalia resemble *Pictothyris*, a genus placed by him (1965) in the Laqueidae. However, the Cainozoic Pacific genus *Jolonica* can be placed in the Laqueidae with some confidence since Cooper (1957) made available an excellent set of photographs of this previously unillustrated type species. *Jolonica* is characterized by free inner hinge plates with a

small cardinal process and a loop with wide medio-vertical connecting bands. That is, *Jolonica* combines the cardinalia of *F. sanguinolenta* with the loop pattern of *Kingena* and *Paral dingia*. In addition the dental plates characteristic of other members of the family are present.

The addition of *Kingena*, *Zittelina*, *Belothyris*, *Frenulina*, *Jolonica*, *Aldingia* and *Paral dingia* to the Laqueidae extends the range of the family from the Upper Jurassic through Tertiary to Recent times. Sufficient extra-Australian forms have not been seen to pronounce on evolutionary trends, but there is a fairly obvious line of succession apparent in the Australian material observed. The Cretaceous species *Kingena mesembrina* (the only species previously described from Australia) seems to be related to the Recent Pacific *Frenulina sanguinolenta* through the Lower Miocene *Paral dingia woodsii* and the Upper Miocene-Pliocene species *Frenulina pumila*. No representatives of this family have been described from either New Zealand or Patagonia.

Family LAQUEIDAE Thomson, 1927

Genus *Frenulina* Dall 1894

Frenulina Dall 1894, *Proc. U.S. natn. Mus.* 17:724.

Frenulina Thomson 1927, *N.Z. Board Sci. & Art, Manual No. 7*: 241-2.

Frenulina Hatai 1936, *Venus*, Kyoto, 6 (1): 2-3.

Frenulina Hatai 1940, *Sci. Rep. Tohoku Univ. Ser. 2*, Geol. 20: 326-7.

Frenulina Hatai 1965, *Treatise on Invertebrate Paleontology*: H842.

TYPE SPECIES: (Original Designation) *Anomia sanguinolenta* Gmelin 1790.

DIAGNOSIS: Anterior commissure rectimarginate to sulcate, deltidial plates discrete to conjunct, foramen submesothyrid to mesothyrid. Cardinalia lamellar, consisting of socket ridges, crural bases, inner hinge plates with free or fused medial borders and a small transverse cardinal process. Loop with two pairs of connecting bands, lateral and latero-vertical and a transverse band with postero-lateral spines. Ventral valve with dental plates and a sessile pedicle collar. STRATIGRAPHIC RANGE: Upper Miocene—Recent.

DISTRIBUTION: Australia (U. Miocene); Okinawa (Pliocene-Pleistocene); Australia, Hawaiian Islands, Philippines, New Caledonia, Indian Ocean, Tonga, Tahiti, Japan, Okinawa (Recent).

COMMENTS: The inclusion in *Frenulina* of the Miocene species *Terebratella pumila* Tate is of interest in extending the vertical distribution of the genus. *F. sanguinolenta* is one of the most widespread of Recent Pacific brachiopods. The species has also been described by Cooper (1957) from Pliocene and Pleistocene limestones of Okinawa, an attribution not included in Hatai's description (1965) of *Frenulina*.

F. sanguinolenta and *F. pumila* are closely related species and show few distinguishing features. Externally *F. sanguinolenta* is characterized by colour

patterns on the valves which may have been present in *F. pumila*. In *F. sanguinolenta* the common condition of the foramen is submesothyrid with nearly conjunct deltidial plates; however the largest specimens from some localities may show a mesothyrid foramen with conjunct deltidial plates. In *F. pumila* the foramen is submesothyrid with discrete deltidial plates in all specimens examined. The internal features, the loop, cardinalia and structures of the ventral valve, are indistinguishable in many specimens. Only one feature, the disposition of the hinge plates, may differentiate the two species internally. In *F. sanguinolenta* the hinge plates show little variation and are, in the vast majority of specimens examined, quite separate from each other ('divided cardinal plate' of Hatai, 1940, p. 327) and display free anterior and medial borders. In rare instances the medial borders of the hinge plates may fuse at their posterior limits i.e. immediately underneath the cardinal process. *F. pumila*, on the other hand, shows considerable variation in the disposition of the hinge plates (Pl. 5, fig. 6-8). The specimens examined display three patterns, no one of which appeared to dominate, and a full range of variants between them. The first of these patterns is the same as that seen in *F. sanguinolenta* i.e. free hinge plates with the median septum tapering off as a low ridge between their medial borders. In the second type seen, the hinge plates are fused medially thus appearing as an excavate shelf under which the low median septum runs. The third pattern is characterized by separate hinge plates the medial borders of which are fused to the valve floor on either side of the median septum, a pattern similar to that seen in *Macandrevia cranium* (Müller).

Frenulina sanguinolenta (Gmelin 1790)

The development of the loop and cardinalia of *F. sanguinolenta* from Masthead Island, is described in an accompanying paper. The Australian specimens conform in all diagnostic features with descriptions of the species from other localities.

OCCURRENCE: The Australian localities from which *F. sanguinolenta* has been collected are listed below. In addition localities outside Australia have been listed, if the material is in Australia and has been observed by the author. The abbreviations WAM, SAM, and NMV represent the Western Australian Museum, the South Australian Museum and the National Museum of Victoria.

South Australia: Fowlers Bay (WAM).

Western Australia: Onslow, 56 m (WAM).

Queensland: Masthead Island, 34-40 m (SAM and NMV).

New Caledonia: (SAM).

Hawaii: Waikiki, 120 m (WAM); Oahu (NMV).

Sulu Archipelago: Tangalan Island in Maluso Bay, 34 m; 1 mile and 050° from Maluso Bay, 52 m; SE. of Balabac Island, Palawan, 60 m; 8.9 miles W. of Cape Melville light, Balabac Island, Palawan, 50-56 m; N. of Siasi Island, 40-42 m; SW. of Malanipa Island, Basilan Straits, 60 m; 3 miles W. of Malanipa

Island, Basilan Straits, 26 m; 9 miles and 133° from Bongoa light, Tawitawi Bay, 26 m (WAM).

Moluccas: The Mariel King Memorial Expedition 1970 collected specimens at present in the care of the Western Australian Museum from the following stations; AM11 50 m, CP1, 28-60 m, KN11 54-92 m, KN111 74-80 m, KN1V 60-62 m, KRV1 30-40 m.

Frenulina pumila (Tate 1899)

(Pl. 5, fig. 1-8)

Terebratella pumila. Tate 1899, *Trans. R. Soc. S. Aust.* 23: 255, Pl. 8, fig. 1.

DESCRIPTION: Shell outline subcircular, unequally bi-convex, the ventral valve deeper. Anterior and lateral commissures rectimarginate; cardinal margin shorter than the greatest breadth of the shell and gently curved. Deltidial plates small, discrete. Palintropes defined by subangular beak ridges. Foramen submesothryid, large, incomplete, lined by a sessile pedicle collar. Beak short, erect.

Dorsal valve with socket ridges posteriorly fused with the borders of the valve, medially merging with the crural bases. Crural bases, thin horizontal bands linking the bases of the socket ridges with the hinge plates. Inner hinge plates lamellar, fused medially for the greater part of their length, with a wide v-shaped anterior border (see following section on variation). Cardinal process narrow, transverse with roughened posterior surface. Median septum thin, extending to an area just posterior to the mid-length of the valve, moderately high anteriorly, gradually losing height posteriorly to terminate as a low ridge on the valve floor underneath the hinge plates. Loop with descending branches with narrow anterior and posterior segments broadening medially to unite with the two pairs of connecting bands; lateral connecting bands narrow, extending from the anterior elevated tip of the septum to fuse laterally with the descending branches and the latero-vertical connecting bands; latero-vertical connecting bands broad, converging slightly posteriorly, their dorsal lines of attachment fused with both the lateral connecting bands (posteriorly) and the descending branches (anteriorly), their ventral lines of attachment fused with the inner borders of the transverse band; transverse band broad with short posteriorly directed spines projecting from its postero-lateral corners.

Ventral valve with small hinge teeth, moderately stout, triangular in outline. Dental plates lamellar, laterally delimiting a pair of cavities, medially confluent with a wide impunctate sheath, the sessile pedicle collar. Pedicle collar thin, longitudinally striated, lining and intimately fused with the posterior cavity of the valve and extending posteriorly to the borders of the foramen.

VARIATION: The external features of this species show little variation apart from slight differences in the degree of convexity of the valves and the anterior commissure which may be rectimarginate or slightly sulcate. However, there is considerable variation in the position and extent of the hinge plates. In some specimens examined the hinge plates present the same appearance as in *F. sanguinolenta*, i.e. narrow, shelf-

like structures extending medially from the fused socket ridges and crural bases, with free anterior and medial borders, their posterior borders fused with the posterior wall of the valve a short distance below the cardinal process. Other specimens of *F. pumila* display medial fusion of the hinge plates so that the area bounded laterally by the combined socket ridges and crural bases and posteriorly by the posterior wall of the valve is occupied by an excavate platform widely separated anteriorly from the valve floor. In such cases the low median septum passes underneath the fused hinge plates and gradually merges with the floor of the valve, sometimes merging also with the under surfaces of the hinge plates. Variants are found which show all degrees of medial fusion of the hinge plates, this apparently taking place in a posterior to anterior direction.

In addition other specimens show fusion of the medial borders of the hinge plates with the valve floor instead of with each other. The hinge plates fuse with the valve floor on either side of the median septum thus giving the appearance of two pockets with anterior openings lying between the septum and the socket ridges.

TYPE MATERIAL: Neotype P17326 (length 10 mm, breadth 9 mm, depth 5 mm) in the Palaeontological Collection of the National Museum of Victoria.

STRATIGRAPHIC RANGE: Mitchellian-Kalimnan.

OCCURRENCE: *Tambo River Formation*; Swan Reach, Victoria.

Jemmys Point Formation: Ritchies cutting on Scrivenors Rd., W. side of Mississippi Creek, Grid Ref. Bairnsdale 878 329. W. side of N. arm, Lakes Entrance, Victoria, 0.9 m above high tide mark, Grid Ref. Bairnsdale 909 278.

COMMENTS: Tate described *F. pumila* from three specimens obtained from 'the Gippsland Lakes'. Tate states that the largest of these specimens was sacrificed to display the internal details. The two syntypes remaining are not present in Tate's collection in the South Australian Museum and are presumed to have been lost. Specimens which conform with Tate's description and his one illustration have been obtained from Swan Reach, Mississippi Creek and Jemmys Point. These localities are in the Gippsland Lakes area and it is known from Dennant (1898) that he and Tate collected at Swan Reach and at Mississippi Creek. Many specimens are available from Swan Reach, a few from the other two localities. The specimens from each locality display dental plates, a loop with two pairs of connecting bands and cardinalia with inner hinge plates and a small cardinal process; externally they agree in the possession of a submesothryid foramen, small discrete deltidial plates and a rectimarginate anterior commissure. The specimens obtained from Mississippi Creek and Jemmys Point however differ externally from those collected at Swan Reach in the degree of convexity of the valves. The valves are fully and evenly convex in the specimens from Swan Reach, specimens from the other localities are less convex in the umbonal areas, a feature noted by Tate.

It is also noteworthy that the deposits at Mississippi

Creek and Jemmys Point are younger in age (Cheltenhamian-Kalimnan) than those at Swan Reach (Mitchellian). Therefore it is possible that two species are represented here. A range of variability in some morphological features is noted above and is based on a collection of nearly 100 specimens from Swan Reach. Only three specimens from Mississippi Creek have been examined and two from Jemmys Point, consequently there is no indication of the variability of different morphological features from these localities. The abundance of material obtainable from Swan Reach makes it desirable that this locality be selected as the type locality for the species. The largest specimen observed by Tate (5 mm in diameter) is approximately half the size of the largest specimens examined from the three localities cited above.

Aldingia Thomson 1916

Aldingia Thomson 1916, *Geol. Mag.* Dec. 6 (3): 501.

Aldingia Thomson 1927, *N.Z. Board Sci. & Art, Manual No. 7*: 230-1.

Aldingia Hatai 1965, *Treatise on Invertebrate Paleontology*: H834.

TYPE SPECIES: (Original Designation) *Terebratella furculifera* Tate 1880.

DIAGNOSIS: Anterior commissure rectimarginate to sulcate, deltidial plates discrete to conjunct, foramen submesothyrid to mesothyrid. Cardinalia thick with socket ridges flanking a solid platform fused anteriorly with the median septum, with a transversely striated area on the posterior segment of the platform serving for the attachment of the diductor muscles. Loop with two pairs of connecting bands, lateral and medio-vertical. Ventral valve with a sessile pedicle collar and hinge teeth supported by swollen bases derived from thickened dental plates.

STRATIGRAPHIC RANGE: Upper Eocene-Recent.

DISTRIBUTION: Australia.

COMMENTS: Thomson (1916, 1927) created the genus *Aldingia* for three species, *Terebratella furculifera* Tate, *Terebratella* (?) *woodsii* Tate, and *Megerlia willemoesi* Davidson, which displays loops with two pairs of connecting bands attached to the septum. *T.* (?) *woodsii* is transferred here to the new genus *Paral dingia*. Thomson referred *Aldingia* to the subfamily Mühlfeldtiinae Oehlert (embracing genera now attributed to the Kraussinidae Dall 1870) stating that the subfamily position is uncertain and that the absence of dental plates in *Aldingia* made relationship with *Frenulina* or *Laqueus* unlikely. The presence of dental plates, associated with a sessile pedicle collar, is described in those species referred to *Paral dingia*. Adult specimens of *Aldingia furculifera* display a sessile pedicle collar confluent anteriorly with swollen bases supporting the hinge teeth. No very young specimens of *A. furculifera* are available but the ventral interior of one young adult (Pl. 5, fig. 13) does indicate that these swollen bases arise as a result of the thickening of early dental plates and their subsequent fusion with the valve walls. Moreover in all specimens in the early adult size range the swollen bases supporting the hinge teeth are

limited to the area immediately beneath the teeth and do not represent a generalized thickening of the lateral walls of the valve.

The species attributed to *Aldingia* and *Paral dingia* are closely related in external characters and in cardinalia and loop patterns. With respect to external characters both genera display rectimarginate to sulcate folding and a submesothyrid to mesothyrid foramen, the deltidial plates are discrete to conjunct in *Aldingia*, discrete in *Paral dingia*. The chief difference between the two genera is the degree of thickness of the elements of the loop, cardinalia and structures of the ventral valve. It is curious that *Aldingia* which displays thick, solid cardinalia possesses a thin lamellar loop while *Paral dingia* with thin lamellar cardinalia displays a loop with thicker, broader, spinous bands.

Aldingia furculifera (Tate 1880)

(Pl. 5, fig. 9-16)

Terebratella furculifera Tate 1880, *Trans. R. Soc. S. Aust.* 3: 161, Pl. 11, figs. 7a-c.

Waldheimia (?) *insolita* Tate (pars) 1880, *Ibid.*: 151-2.

Terebratella furculifera Tate 1899, *Ibid.* 23: 254-5.

Aldingia furculifera Thomson 1916, *Geol. Mag.* 53: 501.

Aldingia furculifera Thomson 1927, *N.Z. Board Sci. & Art, Manual No. 7*: 230-1, fig. 71a.

DESCRIPTION: Shell outline broadly ovate, the greatest width at mid-length; uncequally biconvex, the ventral valve slightly deeper and slightly carinate, dorsal valve evenly convex. Anterior and lateral commissures rectimarginate, cardinal margin terebratulid. Deltidial plates small, discrete, separated by a narrow fissure medially. Foramen submesothyrid, incomplete with a slight notch anteriorly marking the line of separation of the deltidial plates. Beak short, nearly erect.

Dorsal valve interior with posterior region thickened to form a platform in which the sockets are countersunk laterally. Socket ridges moderately thick, straight, converging posteriorly to fuse with the valve borders, anteriorly overhanging the sockets, sloping fairly steeply downwards medially. Crural bases visible as slightly swollen areas at the bases of the medial slopes of the socket ridges and extending for approximately the anterior halves of the lengths of the socket ridges. Hinge platform solid, slightly concave; posterior region of platform delimited as transversely striated area in the shape of a quadrant of a circle, representing posterior surface of the cardinal process and serving for the attachment of the diductor muscles; immediately anterior to this area two ovate scars of the dorsal pedicle muscles are visible. Median septum moderately thick, very short, extending anteriorly for a distance approximately equal to the length of the hinge platform, tapering sharply away anteriorly. Loop with slender branches and bands; the transverse band excavated medially leaving the wide posterolateral projections. Adductor muscle impressions fairly deep, ovate scars extending from the base of the hinge platform to areas just beyond the anterior tip of the septum.

Ventral valve with thick hinge teeth under which lie grooves for the reception of socket ridges. Lateral valve walls thickened in a localized area immediately ventral to the hinge teeth and grooves. A slight ridge extends across the floor of the valve between the posterior terminations of the lateral thickened areas and marks the anterior border of the sessile pedicle collar.

TYPE MATERIAL: Eleven syntypes, T895 A-K, in the Ralph Tate Collection, South Australian Museum, of which T895H (length 14 mm, breadth 12 mm, depth 5.5 mm) is selected as the lectotype.

TYPE LOCALITY: Tortachilla Limestone, Blanche Point, South Australia.

STRATIGRAPHIC RANGE: Aldingan-Janjukian.

OCCURRENCE: *South Australia:* Tortachilla Limestone (Aldingan): Blanche Point, Maslin Bay and Christie's Beach, Aldinga; Port Noarlunga. *Blanche Point Marls:* Blanche Point, Aldinga.

Western Australia: Wilson Bluff Limestone (Aldingan): Bunda Cliffs, Great Australian Bight.

Victoria: Browns Creek Clay (Aldingan): Washout 1, immediately NW. of the mount of Browns Creek, Grid Ref. Aire 277 177; Washout 11, nearest mouth of Johanna River, uppermost horizon in forked gully, Grid Ref. Aire 276 179. *Castle Cove Limestone* (Aldingan): Geological survey locality Aw5, Grid Ref. Aire 307 162. *Glen Aire Clay* (Aldingan): Geological Survey locality Aw1, outcrop nearest Point Flinders at 'waterfall', Grid Ref. Aire 368 096. *Calder River Limestone* (Janjukian): Geological Survey locality Aw4, anticline on Airc Coast, near Middle Beach, Glen Aire.

COMMENTS: *A. furculifera* was first described by Tate (1880) from six syntypes collected from the Tortachilla limestone, at Blanche Point, Aldinga. Tate's collection in the South Australian Museum includes a card bearing 11 specimens (T895A-K) and labelled *Terebratella furculifera*. The largest of these specimens (T895-H) has a length of 14 mm, breadth of 12 mm, depth of 5.5 mm and like the other syntypes displays a submesothryd foramen and discrete deltidial plates. Internally the valves are thickened posteriorly in the hinge platform area of the dorsal valve and in the lateral walls of the ventral valve immediately underneath the hinge teeth. The remaining parts of the valves are relatively thin without noticeable muscle or pallial sinus markings.

In the same paper Tate described the species *Waldheimia* (?) *insolita* from a collection of specimens obtained from 'a marly band in Blanche Point Cliff, Aldinga'. (p. 152). A group of specimens on a card in Tate's type collection are labelled '*Waldheimia insolita*, Aldinga Bay' and are numbered T908A-E-G-H. With the exception of T908A these specimens are still regarded as members of the species *insolita* (a magadinid species). Specimen T908A differs from the remaining material externally (Pl. 5, fig. 14). in displaying a mesothryd foramen and conjunct deltidial plates. Since the valves lie loosely one upon the other internal details could also be studied. (Pl. 5, fig. 15-16). The cardinalia bear a close resemblance to these structures in the material described by Tate as

A. furculifera from Blanche Point; the loop is broken but the remains of two pairs of connecting bands are seen on the crest of the septum. This specimen differs from the Blanche Point syntypes of *A. furculifera* in possessing a mesothryd foramen, conjunct deltidial plates, thick valves with prominent muscle and pallial sinus markings and in its larger size (length 28 mm, breadth 20 mm). Since both the smaller and the larger forms have been collected from the Blanche Point Marls it seems likely that the species *A. furculifera* is described from young adult forms and that specimen T908A represents the adult form. If this is so then the transition from a submesothryd to a mesothryd foramen and from discrete to conjunct deltidial plates occurs at a relatively late stage of development although a similar developmental pattern may be seen in other genera including *Frenulina*.

Again in 1880 Tate referred to *Waldheimia* (?) *insolita* a group of specimens (T899A-F) from Wilson's Bluff limestone, Great Australian Bight. Tate (1899, p. 254) stated that these specimens 'prove on dissection to belong to *Terebratella* and to the species *furculifera*'. Since these specimens also show conjunct deltidial plates (foramen remains submesothryd), thicker valves, and display an average length of 23 mm it does give further weight to the attribution of T908A as the adult form of *A. furculifera* and of specimens T895A-K as a collection of young adults. Although *insolita* has page priority, under Recommendation 24A of the International Code of Zoological Nomenclature the name *furculifera* has been chosen for this species.

Aldingia willemoesi (Davidson 1878)

Megerlia willemoesi Davidson 1878, *Proc. R. Soc. Lond.* 27: 438-9.

Megerlia willemoesi Davidson 1880, *Rep. Voy. H.M.S. Challenger*, Zool. Vol. 1, Brachiopoda: 51-2, Pl. 4, figs. 1-3.

Megerlia willemoesi Davidson 1886, *Trans. Linn. Soc. Lond.* 4(2) Zool: 111, Pl. 19, figs. 23-26.

Megerlia willemoesi Tate 1886, *Trans. R. Soc. S. Aust.* 9: 110-1.

Aldingia willemoesi Thomson 1927, *N.Z. Board Sci. & Art*, Manual No. 7: 230-1, fig. 71b.

COMMENTS: The only specimens of *A. willemoesi* described are those collected by the Challenger Expedition at 240 metres off Twofold Bay, South Australia and one dead shell recorded by Tate from 44 m at Encounter Bay, South Australia. Davidson gave a brief diagnosis of the species in 1878 and in the Challenger Reports of 1880 printed a fuller description. From this description and the accompanying illustrations the species appears to be slightly sulcate in folding and to possess fused deltidial plates; the foraminal position and the type of cardinalia are difficult to estimate. Therefore the species is referred to *Aldingia* with some doubt. The loop, in displaying two pairs of connecting bands, lateral and medio-vertical, is typical of both *Aldingia* and *Paralidingia*.

Paralidingia gen. nov.

TYPE SPECIES: *Terebratella* (?) *woodsii* Tate 1880.

DIAGNOSIS: Anterior commissure rectimarginate to

sulcate, deltidial plates discrete, foramen submesothyrud to mesothyrud. Cardinalia lamellar with excavate, inner hinge plates fused medially and continuous posteriorly with a transversely striated area serving for the attachment for the diductor muscles. Loop with wide, lamellar ascending and descending branches, a thick transverse band with postero-lateral flanges and stout lateral and medio-ventral connecting bands. Ventral valve with dental plates and a sessile pedicle collar.

STRATIGRAPHIC RANGE: Upper Eocene—Lower Miocene.

DISTRIBUTION: Australia.

COMMENTS: The genus *Paral dingia* is erected for species which differ from *Aldingia* in the possession of discrete dental plates, excavate inner hinge plates and a loop with broad and moderately thick connecting bands. The relationships between the two genera are discussed in the comments on *Aldingia*.

The species *P. woodsii* and *P. tepperi* differ in outline, folding and foraminal position. *P. woodsii* is sub-pentagonal in outline with a sulcate anterior commissure and a submesothyrud foramen, *P. tepperi* is subcircular, rectimarginate and mesothyrud. *Terebratella pentagonalis* is provisionally referred to the genus from the external characters of a single specimen which is similar to *P. woodsii* in folding and foraminal position. The two species differ only in the degree of convexity of the valves and in folding. In *P. pentagonalis* the anterior commissure is rectimarginate and the valves show a greater degree of convexity than is the case in *P. woodsii*.

Paral dingia woodsii (Tate 1880)

(Pl. 6, fig. 4-8)

Waldheimia corioensis Tenison Woods 1877, *J. Proc. R. Soc. N.S.W.* 11: 78-9, figs. 3a-c. (non *Waldheimia corioensis* McCoy).

Terebratella (?) *woodsii* Tate 1880, *Trans. R. Soc. S. Aust.* 3: 161-2, pl. 9, figs. 10a-c.

Terebratella woodsii Tate 1899, *Ibid.* 23: 255.

Aldingia woodsii Thomson 1927, *N.Z. Board Sci. & Art Manual No. 7*: 231.

DESCRIPTION: Shell outline broadly subpentagonal, greatest width lying at midlength; unequally biconvex, dorsal valve slightly convex with a median sulcus gradually widening anteriorly and extending from the umbo to the anterior border of the valve, ventral valve deeper with a prominent median carina. Anterior commissure sulcate, lateral commissures sinuate; cardinal margin terebratulid. Deltidial plates discrete. Palintropes defined by subangular beak ridges. Foramen submesothyrud, incomplete, slightly marginate, lined with a sessile pedicle collar. Beak short, suberect.

Dorsal valve interior with short, straight socket ridges converging slightly posteriorly and fused with the borders of the valve, anteriorly overhanging deep sockets. Crural bases fused with the socket ridges, appearing anteriorly as slight ridges at the medial bases of the socket ridges. Hinge plates lamellar, excavate, short, fused laterally with the crural bases and sloping fairly steeply medially to fuse with each

other on top of the median septum, anteriorly the hinge plates extend forwards slightly further laterally than medially; a low, longitudinal ridge extends along the mid-line of the posterior two-thirds of the length of the fused hinge plates. Posterior border of hinge plates marked by a slight subarcuate ridge, between this ridge and the dorsal umbo the hinge platform is transversely striated, this area presumably serving for the attachment of the diductor muscles. Median septum thin with a rounded free edge, extending to a point approximately one-third the total length of the valve from its posterior tip, low posteriorly, gradually increasing in height anteriorly and terminating abruptly. Loop with crura short, fairly stout, rounded; crural processes tapering to low points directed medially; descending branches wide with short thorn-shaped processes scattered along the anterior halves of their laterally-directed free edges, midway along their length attached to the anterior crest of the median septum by moderately wide lateral connecting bands; ascending branches and transverse band lamellar and wide, the postero-lateral corners of the transverse band extended by a pair of tapering flanges which are continuous dorsally with a pair of thick connecting bands running to the anterior crest of the septum; thick longitudinal ridges mark the surface of the transverse band and extend from its anterior border to the posterior borders of the flanges.

Ventral interior with small, moderately thick hinge teeth, subcircular in outline. Dental plates lamellar, confluent with the bases of the hinge teeth and descending to the floor of the valve thus delimiting two small lateral cavities; dorsally and posteriorly confluent with a wide, impunctate sheath, the sessile pedicle collar.

TYPE MATERIAL: Five syntypes T901A-E in the Ralph Tate Collection, South Australian Museum, of which T901A (length 11 mm, breadth 11 mm, depth 5 mm) is selected as the lectotype.

TYPE LOCALITY: *Freestone Cove Sandstone*; Table Cape, Tasmania (Lower Miocene).

Paral dingia tepperi (Tate 1880)

(Pl. 6, fig. 11-14)

Terebratella tepperi Tate 1880, *Trans. R. Soc. S. Aust.* 3: 160, Pl. 9, figs. 8a-c.

? *Terebratella tepperi* Thomson 1927, *N.Z. Board Sci. & Art, Manual No. 7*: 293.

DESCRIPTION: Shell outline subcircular, greatest width lying at mid-length; unequally biconvex, the dorsal valve moderately and evenly convex, ventral valve slightly deeper with a slight median carina over the posterior half of the valve. Anterior and lateral commissures rectimarginate; cardinal margin broad and gently curved. Deltidial plates discrete, small. Palintropes wide, defined by rounded beak ridges. Foramen round, mesothyrud, incomplete, marginate, lined by a sessile pedicle collar. Beak suberect.

The cardinalia of the dorsal valve resemble these structures in *P. woodsii*, the only difference lying in the outline of the anterior border of the hinge plates. This border is straight in *P. tepperi* and medially indented in *P. woodsii*. The loop is broken in the

only dorsal valve of *P. tepperi* observed, however the edges of two pairs of connecting bands are visible on the anterior crest of the septum.

TYPE MATERIAL: Five syntypes T896A-E in the Ralph Tate Collection, South Australian Museum, of which T896C (length 21 mm, breadth 20 mm, depth 11 mm) is selected as the lectotype.

TYPE LOCALITY: *Muloowurtie Clays*: near Ardrossan, Yorke Peninsula, South Australia. (Upper Eocene.)

***Paral dingia pentagonalis* (Tate 1880)**
(Pl. 6, fig. 9, 10)

Terebratella (?) *pentagonalis* Tate 1880, *Trans. R. Soc. S. Aust.* 3: 161, Pl. 9, figs. 5a-b.

(?) *Terebratella* (?) *pentagonalis* Thomson 1927, *N.Z. Board Sci. & Art Manual* No. 7: 293.

DESCRIPTION: Shell outline subpentagonal, the greatest width lying slightly anterior to mid-length; unequally biconvex, the ventral valve deeper, both valves displaying a slight median depression over the anterior halves of their lengths. Anterior and lateral commissures rectimarginate; cardinal margin terebratulid. Beak ridges rounded defining wide palintropes. Deltidial plates discrete, small. Foramen submesothyrid. Beak short, erect.

TYPE MATERIAL: Holotype T883 (length 17 mm, breadth 13 mm, depth 9 mm) in the Ralph Tate Collection, South Australian Museum.

TYPE LOCALITY: *Tortachilla Limestone*: Maslin Bay, Aldinga, South Australia.

STRATIGRAPHIC RANGE: Aldingan (Upper Eocene).

COMMENTS: Tate erected the species *pentagonalis* from two specimens, only one of which is preserved in his Collection. This species bears a close external resemblance to *P. woodsii* and on this basis is referred to the genus. The two species possess a submesothyrid foramen, discrete deltidial plates and a terebratulid cardinal margin. They differ in the degree of convexity of the valves and in folding. *P. woodsii* displays a sulcate anterior commissure and slightly convex valves with a pronounced carina and sulcus in the ventral and dorsal valves respectively. *P. pentagonalis*

is moderately and evenly biconvex with a rectimarginate anterior commissure.

ACKNOWLEDGMENTS

I wish to thank the Director and Staff of the National Museum of Victoria for providing the facilities to work with the Collections in their care and the additional help of Mr. T. A. Darragh in the provision of statigraphical data.

The Western Australian Museum, the Department of Geology, University of Adelaide and the South Australian Museum generously made available on loan any brachiopod specimens requested. Mr. Frank Guy of the Royal Melbourne Institute of Technology took the photographs, the cost of which was covered by a grant from the CSIRO Science and Industry Endowment Fund.

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EXPLANATION OF PLATES

PLATE 5

Frenulina pumila (Tate)

- FIG. 1-3—Dorsal, anterior and lateral views of P17236 (National Museum of Victoria) neotype, $\times 3$.
 FIG. 4—Ventral valve interior, $\times 3$.
 FIG. 5—Dorsal valve interior showing loop. One of the dental plates is visible projecting from the top left hand corner of the broken ventral valve, $\times 4$.
 FIG. 6-8—Dorsal valve interiors showing differences in different specimens in the extent of hinge plates, $\times 10$.
 Tambo River Formation, Swan Reach, Victoria.

Aldingia furculifera (Tate)

- FIG. 9, 10—Dorsal and lateral views of T895H (Ralph Tate Collection, South Australian Museum), lectotype, $\times 1\frac{1}{2}$.
 FIG. 11—Dorsal valve interior, $\times 5$.
 FIG. 12—Anterior view of dorsal valve interior, $\times 5$.
 FIG. 13—Anterior view of internal hinge area to show dental plates in young specimen, $\times 4$.
 Tortachilla Limestone, Blanche Pt., Aldinga, South Australia.
 FIG. 14—Dorsal view of specimen T908A in the Ralph Tate Collection, South Australian Museum, $\times 1\frac{1}{2}$.
 FIG. 15, 16—Respectively dorsal and ventral valve interiors of specimen T908A in the Ralph Tate Collection, South Australian Museum, $\times 1\frac{1}{2}$.
 Blanche Point Marls, Blanche Pt., Aldinga, S.A.
 All specimens with the exception of those represented in Figs. 1-3, 14-16, coated with magnesium chloride.

PLATE 6

Kingenia mesembrina (Etheridge)

- FIG. 1-3—Dorsal valve interior; ventral, lateral and anterior views of hypotype in the collection of the Geology Department, University of Western Australia and figured by Elliott (1952, Pl. 1, fig. 4), $\times 5$.
 Gingin Chalk, Western Australia.

Paral dingia woodsii (Tate)

- FIG. 4-6—Dorsal valve interior; ventral, lateral and anterior views, $\times 5$.
 FIG. 7, 8—Dorsal and lateral views of T901A, lectotype, Ralph Tate Collection, South Australian Museum, $\times 2\frac{1}{2}$.
 Freestone Cove Sandstone, Table Cape, Tasmania.

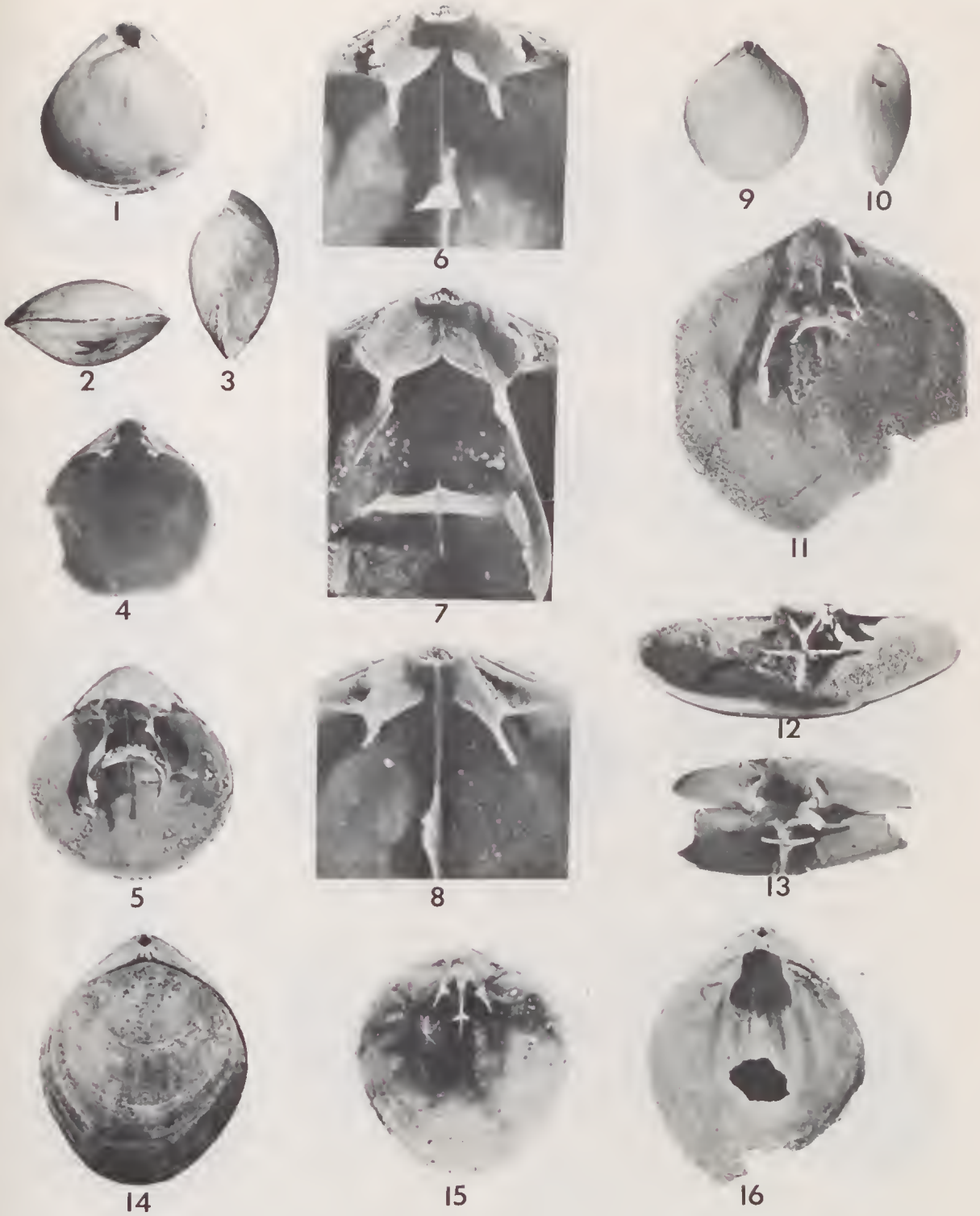
Paral dingia pentagonalis (Tate)

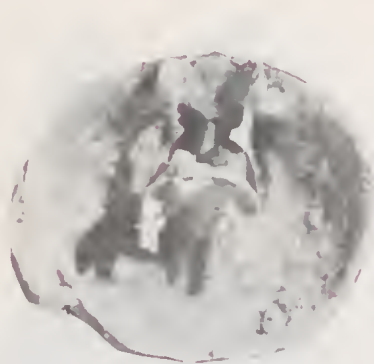
- FIG. 9, 10—Dorsal and lateral views of T883, holotype, Ralph Tate Collection, South Australian Museum, $\times 2$.
 Tortachilla Limestone, Maslin Bay, Aldinga, South Australia.

Paral dingia tepperi (Tate)

- FIG. 11—Dorsal interior of T896A, syntype, Ralph Tate Collection, South Australian Museum, $\times 4$.
 FIG. 12, 13—Dorsal and lateral views of T896C, lectotype, Ralph Tate Collection, South Australian Museum, $\times 1\frac{1}{2}$.
 FIG. 14—Anterior view of ventral interior of T896B, syntype, Ralph Tate Collection, South Australian Museum, $\times 4$.
 Mulloowurtie Clays, near Ardrossan, Yorke Peninsula, South Australia.

All specimens with the exception of those represented in Fig. 4-6 coated with magnesium oxide.

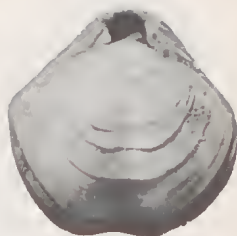




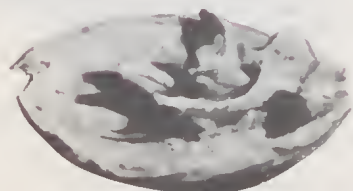
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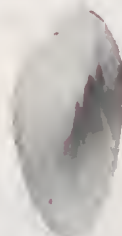
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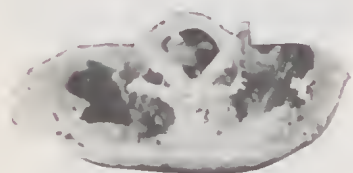
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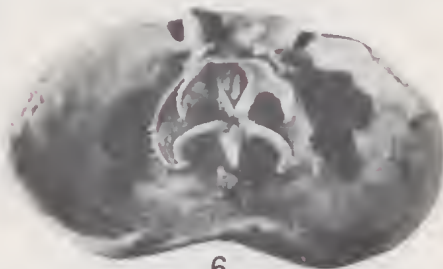
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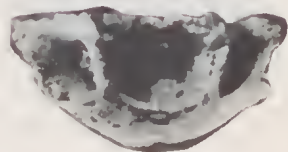
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STUDIES ON AUSTRALIAN CAINOZOIC BRACHIOPODS

3. THE SUBFAMILY BOUCHARDIINAE (TEREBRATELLIDAE)

By JOYCE R. RICHARDSON*

ABSTRACT: The Australian Tertiary species *Malleia portlandica* (Chapman 1913) is re-described and *Malleia* is transferred from the Neothyridinae to the Bouchardiinae. The Bouchardiinae and the monotypic genera *Malleia* and *Neobouchardia* are all re-defined.

INTRODUCTION

A revision of Australian Cainozoic brachiopods is in progress and, for comparative purposes, Mesozoic and New Zealand genera are being examined wherever possible. This work is concerned with the structures which are of prime importance in classification, namely the developmental and adult patterns of the loop, and adult patterns of the cardinalia. The bulk of material available is attributable to the family Terebratellidae which is composed, almost exclusively, of austral forms. The classification of the family is so unwieldy that it is desirable for the genera to be re-arranged in more workable subfamily groupings indicating, if not true phyletic relationships, at least some more coherent picture of apparent similarities.

The subfamily Bouchardiinae is represented in Australia by two species, *Neobouchardia minima* (Thomson 1918) from the Oligocene of Victoria and *Bouchardiella cretacea* Etheridge (1913) from Upper Cretaceous beds of Western Australia, and it is proposed that the genus *Malleia* be transferred to the Bouchardiinae from the Neothyridinae. To place *Malleia* in the Bouchardiinae involves changing the diagnosis of both the subfamily Bouchardiinae and the genus *Malleia*. For it is proposed that, to a group of genera which agree in foramen position (epithyrid), type of deltidial plate (fused, not delimited within the palintrope) and in the possession of a solid hinge platform without hinge trough or bifurcating septum, a genus be added with a hypothyrid foramen, discrete deltidial plates and alleged by Thomson (1927) and Allan (1940) to possess a hinge trough and a bifurcating septum.

That the four genera now assigned to this subfamily form a related group is suggested by the number of features which they bear in common,

and which are also unique to the subfamily i.e. cardinalia consisting of socket ridges and a cardinal process of distinctive shape, a high median septum which does not unite with the cardinalia, and no loop. Those features in which they differ (foraminal position, type of deltidial plate, extent of thickening of cardinalia) seem to be related to the loss of the supportive function of the pedicle and are not considered to be of significance at the subfamily level.

Subfamily BOUCHARDIINAE Allan, 1940
Emend. nov.

DIAGNOSIS: Terebratellidae with cardinalia consisting of socket ridges and a cardinal process; with a high median septum which may bear lamellae and which is not connected with the cardinalia; with sulcate folding, hypothyrid or epithyrid foramina and discrete or fused deltidial plates.

KEY TO GENERA

- | | |
|---|----------------------|
| Foramen hypothyrid, deltidial plates discrete, socket ridges and cardinal process defined | <i>Malleia</i> |
| Foramen minute and epithyrid, deltidial plates fused and not delimited within the palintrope, cardinalia fused into solid platform: | |
| 1. anterior rim of cardinal process fully indented | <i>Bouchardia</i> |
| 2. anterior rim of cardinal process partially indented: | |
| a. lamellae on septum | <i>Bouchardiella</i> |
| b. boss on septum | <i>Neobouchardia</i> |

DISCUSSION: Allan (1940) created the subfamily Bouchardiinae for three genera (*Bouchardiella*, *Bouchardia*, *Neobouchardia*) which Thomson (1927, p. 271) had noted 'present certain characters in common which sharply distinguished them from other rostrate Telotremata'. Allan's diagnosis, which was adopted by Hatai and Elliott (1965), states that in

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these genera 'the crural bases unite in a hinge-platform, the septum is unbifurcated, there is no hinge-trough' (p. 270).

In the present paper, the monotypic genus *Malleia* is transferred from the subfamily Neothyridinae to the Bouchardiinae. *Malleia* was assigned by Allan (1940) to the Neothyridinae on the basis of a broadly bifurcating septum and a long, broad hinge trough. A subsequent paper will discuss forms exhibiting hinge plates in association with an apparently bifurcating septum. Hinge plates are not present in *Malleia*, nor does the septum bifurcate. As described in detail for *Malleia portlandica* (Chapman 1913), the floor of the dorsal valve bears oblique ridges extending from the bases of the socket ridges to the mid-line of the valve. These ridges give the appearance of marking the posterior limits of the adductor muscle scars in those specimens in which the scars are well defined (Pl. 7, fig. 6). Also in many specimens the low ridge marking the posterior limit of the median septum extends further posteriorly than the posterior limits of these ridges. Since the median septum of *Malleia* does not bifurcate and furthermore does not unite with the cardinalia, that area of the shell previously termed the 'hinge trough' is merely the posterior floor of the dorsal valve which is continuous with a cavity or cave underlying the cardinal process.

The Bouchardiinae display a solid hinge platform which apparently consists of thick socket ridges fused with a large cardinal process. It is difficult to describe the cardinal processes seen in the Terebratellidae without distinguishing the anterior and posterior surfaces indentified by Thomson (1927) but not defined in the Treatise (1965). Consequently the following definition is included herein.

The cardinal process is a median unpaired process lying at the posterior end of the interior of the dorsal valve and serves for the attachment of the dorsal ends of the diductor muscles. The cardinal process commonly displays two different types of surface—a flattened (or concave), striated (or roughened) surface and a smooth, commonly convex, surface. The striated surface faces ventrally and, to a varying degree, posteriorly and is termed the posterior surface. The smooth surface, termed the anterior surface, may extend below the posterior surface and thus face dorsally or it may be expanded to form a conical or globular process facing largely anteriorly. The rim of the cardinal process is the line of junction of the anterior and posterior surfaces.

Thomson (1927, p. 88) defines a transverse cardinal process as one which is broader than long and in which the striated or roughened surface is most prominent and faces nearly ventrally.

The cardinal process of the Bouchardiinae is unlike that seen in any other members of the Terebratellidae (Pl. 7, fig. 2, 6-8). It is most easily described as the derivative of a shallow, rimmed bowl with an inner, roughened concave surface representing the posterior surface and an outer smooth, convex surface representing the anterior surface of the cardinal process. The anterior rim of this bowl now becomes indented medially and moves pos-

teriorly to fuse with the medial region of the posterior rim thus presenting the surface appearance of two lateral pockets on either side of a median indentation. The lateral pockets extend obliquely from the median posterior region of the cardinal process thus giving the inverted V-shaped appearance to the cardinal process described by Davidson (1887, p. 116) and Thomson (1927, p. 273). The cardinal process of *Neobouchardia* shows the first stage of folding (i.e. the median indentation of the anterior rim) which culminates in the complete fusion of the anterior and posterior rims of the cardinal processes in *Bouchardia* and *Malleia*. In *Bouchardia* the posterior regions of both valves are greatly thickened and the cardinal process is fused with the floor of the valve; the cardinal process of *Malleia* does not fuse with the dorsal valve floor and the cavity underlying it is continuous anteriorly with the remainder of the valve floor. These cavities or caves underlying regions of the cardinalia are a characteristic feature of the Bouchardiinae and their extent is governed by the amount of secondary thickening which has occurred in the posterior segment of the dorsal valve. Thus in *Malleia* one large cave is delimited posteriorly by the dorsal umbo region, laterally by the socket ridges and ventrally by the dorsal surface of the cardinal process. In the remaining three genera the anterior surface of the base of the hinge platform is marked by two or more shallow caves.

In his diagnosis of the subfamily Allan (1940, p. 270) states that 'the crural bases unite in a hinge platform'. Neither crural bases nor crura are recognizable in *Malleia* nor have they been described in any of the species attributed to the remaining three genera of the Bouchardiinae. It is possible that crural bases are present but are so intimately fused with other elements of the cardinalia that they are unidentifiable as separate structures. However, until the study of youthful forms of any of the species demonstrates their presence and later fusion with other elements, it seems inadvisable to describe the presence of crural bases as characteristic of the Bouchardiinae. Since none of the genera attributed to the Bouchardiinae are described as possessing crura, the existence of crural bases seems unlikely.

None of the species attributed to the Bouchardiinae possesses a loop: they all display a high plate-like median septum which tapers off abruptly posteriorly and does not unite with the cardinalia. The genera vary in the type of structure attached to the septum. In *Neobouchardia* a small swollen boss lies on the posterior end of the elevated part of the septum. *Bouchardia* and *Bouchardiella* are characterized by curved lamellae, which do not unite, extending from the septum. There are no descending branches apparent in these genera. The septum of *Malleia* exhibits curved lamellae, similar to those of *Bouchardia* and *Bouchardiella*, and, between these lamellae and the valve floor, small triangular plates extend from the septum representing either the rudiments or the only portions remaining of descending branches. A noteworthy feature of the curved lamellae of *Malleia* is their position on the septum. The oblique lines of attachment of the lamellae extend, not from the lateral margins of the

crest of the septum as is characteristic of other members of the Terebratellidae but from the sides of the septum at its approximate mid-height. Elliott (1952) describes the curved lamella of *Bouchardiella cretacea* as arising just below the summit of the septum and the same condition seems to be characteristic of *Bouchardia rosea* as described by Davidson (1850, 1887).

Some comment upon *Bouchardiella cretacea* in relation to other members of the Bouchardiinae is appropriate. *Bouchardiella patagonica* (Ihering 1903), the type species, is not well documented and is stated (Doello-Jurado 1922, p. 200) to differ from *Bouchardia* only in the less advanced cardinal process, a feature which Thomson (1927) regarded as hardly worthy of generic rank. Neither specimens nor figures of *B. patagonica* have been examined either by the writer or by Elliott who emended the diagnosis of the genus (1965) to include *B. cretacea* from Upper Cretaceous beds of Western Australia. Elliott (1952) describes the posterior surface of the cardinal process of *B. cretacea* as a shallow, heart-shaped muscle-pit with anterior indentation. From his description the cardinal process seemed similar to that of *Neobouchardia*. However, judging from topotypes the cardinal process is almost identical with that of *Magadina cumingi* (Davidson 1852). In all other features *B. cretacea* is closely related to other members of the Bouchardiinae and as Elliott states 'appears to be a form very near the ancestral junction of the Bouchardiinae and Magasinae' (1952, p. 13).

Two factors appear to be responsible for the morphological features characteristic of the Bouchardiinae. First, as a result of possessing only early ontogenetic loop structures (the structures giving rise to the adult loop in other terebratellids) two bouchardiform features must follow i.e. the septum is not associated with the cardinalia and, in the absence of crura, crural bases are not apparent. In other subfamilies of the Terebratellidae crural bases and sometimes hinge plates contribute to the hinge platform in addition to the socket ridges and the cardinal process. The absence of these additional elements of the cardinalia is probably the reason for the presence of caves in areas of the hinge platform. The second factor is that all members of the Bouchardiinae, with the exception of *Malleia*, display great thickening of the posterior regions of both valves. This condition allied with the presence of a tiny foramen occurs in many brachiopods and has been discussed by Rudwick (1970). He points out that posterior weighting of the shell can maintain its stability, that this may occur even in shells with a functional pedicle, but that its importance, and the extent of weighting, increases as the pedicle becomes reduced and can fulfil only a tethering function. Atrophy of the pedicle and foramen implies a free-lying habit and reliance on posterior weighting as a shell stabilizer.

In the course of these studies a number of Cainozoic brachiopods from different families have been examined and the presence of a small or atrophied foramen is associated invariably with great thickening in the posterior regions of the valves. The absence

of excessive thickening in *Malleia* is related to the other features in which this genus differs from the remaining members of the subfamily i.e. the easier identification of the components of the cardinalia, a foramen of functional size, discrete deltidial plates and perhaps the more extensive development of septal structures.

From three dried specimens (from Zanzibar and the Gulf of Aden) Muir-Wood (1959) described the new genus and species *Leptothyris ignota* (now *Leptothyrella* as *Leptothyris* is preoccupied). Muir-Wood presumed these specimens to be immature and states 'owing to the spirolophus lophophore and the immature form of the loop it is quite impossible to assign *Leptothyris ignota* to any family of the suborder Terebratelloidea' (p. 309). It may be worth examining *Leptothyrella* in relationship to *Malleia*. As far as one can judge from Muir-Wood's descriptions certain similarities exist between the two genera in external features, type of cardinalia and the form of the median septum. The immature form of the loop forms no obstacle to relationship with the Bouchardiinae as the lophophore is unknown for any member of the subfamily.

Malleia Thomson 1927

Malleia Thomson 1927, N.Z. Board Sci. & Art. Manual No. 7: 283-4.

Malleia Hatai 1965, *Treatise on Invertebrate Paleontology*, H854-5.

TYPE SPECIES: (Original Designation) *Terebratella portlandica* Chapman 1913.

DIAGNOSIS: Plano-convex Bouchardiinae with hypothryd foramen and discrete deltidial plates; with the posterior surface of the cardinal process visible as two posteriorly converging pockets; with a median septum which bears two curved lamellae and rudimentary descending branches.

STRATIGRAPHIC RANGE: Oligocene-Pliocene.

DISTRIBUTION: Australia.

COMMENTS: Thomson erected the genus *Malleia* for *Terebratella portlandica* on the basis of its hypothryd foramen, wide hinge trough and primitive loop. Allan (1940, p. 273) referred the genus to his subfamily Neothyridinae stating that *Malleia* is a primitive member of the group in its foraminal position and loop stage; 'the septum, however, is broadly bifurcating and the hinge-trough long and broad'.

In the following description of the species it is noted that oblique ridges extend between the anterior bases of the socket ridges and the mid-line of the dorsal valve. One of the variable features of the species is the degree of definition of adductor muscle scars. In specimens in which these are well-defined the oblique ridges on the valve floor do not appear as distinct structures but as the posterior borders of the adductor scars. Since the medial limits of these ridges frequently terminate just short of the mid-line of the valve and since the median septum continues as a low ridge beyond their posterior and medial limits, it is unlikely that they could represent the bifurcation of the septum. Since the term 'hinge trough' is defined (Treatise 1965, p. H146) with reference to a bifurcating septum in

association with hinge plates, the lack of either structure in *Malleia* invalidates its use to describe the posterior dorsal valve floor.

Malleia portlandica is described in detail below, because the illustrations of this species in neither Chapman's paper (1913) nor in Thomson's book (1927) give an accurate representation of the disposition of the cardinalia and the septum.

***Malleia portlandica* (Chapman 1913)**

(Pl. 7, fig. 1-6)

Terebratella portlandica Chapman 1913, *Proc. R. Soc. Vict.* 26 (2): 187, Pl. 18, fig. 36a-c, 37, 38.

Terebratella portlandica Chapman 1916, *Rec. Geol. Surv. Vict.* 3 (4): 387, Pl. 65, fig. 36-38.

Malleia portlandica Thomson 1927, *N.Z. Board Sc. & Art, Manual No. 7*: 283-4, fig. 96a-e.

DESCRIPTION: Shell outline subcircular, plano-convex, dorsal valve with short anterior sulcation, ventral valve slightly carinate. Anterior commissure sulcate, lateral commissures rectimarginate, cardinal margin short, slightly curved. Beak ridges subangular, defining short, narrow palintropes. Deltidial plates discrete, small, edging antero-lateral corners of the foramen. Foramen hypothyrid, lined with thin, sessile pedicle collar.

Dorsal valve with strong, straight socket ridges projecting beyond dorsal umbo for approximately one quarter their total length; anteriorly bases of socket ridges confluent with a pair of low ridges extending obliquely in an antero-medial direction to areas just short of mid-line of valve. Cardinal process large, lying between socket ridges and extending from dorsal umbo to points just anterior to mid-length of socket ridges. Ventral surface of cardinal process indented by an inverted V-shaped roughened depression bordered by a rim, this depression appearing to represent the surface of invaginated posterior surface of cardinal process. The cardinal process fused posteriorly with dorsal umbo and laterally with socket ridges but not fused with floor of valve, thus delimiting posterior cave, the roof formed by cardinal process, the sides by socket ridges and the floor by valve floor. Median septum high, wedge-shaped in lateral outline with ventral border slightly longer than attached dorsal border, anterior limit just anterior to mid-length of valve, posteriorly merging with valve floor as low ridge just anterior to hinge platform. Lines of attachment only of lamellar structures attached to septum visible in paratype. However, structures attached to septum apparent in a number of specimens from different localities; these specimens display two curved lamellae, broad at their lines of attachment and narrowing to a point as they curve posteriorly and medially and inserted at approximate mid-height of the septum. Between insertions of lamellae and base of septum two small triangular plates extend from sides of the septum, apparently representing rudiments of descending branches. Adductor muscle impressions, large elongate-ovate scars within which anterior and posterior adductor impressions cannot be separated, anterior limits lying slightly anterior to mid-length

of valve, posteriorly muscles appear to be delimited by low, oblique ridges extending medially from socket ridge bases.

Ventral valve with hinge teeth, strong, rounded and transversely striated. Deep grooves lie immediately beneath hinge teeth for reception of socket ridges. Lateral and posterior walls not thickened. Sessile pedicle collar thin, lining interior of umbo and under-surfaces of deltidial plates. Muscle scars not apparent. Median longitudinal ridge extends from an area level with posterior limits of hinge teeth to a point just posterior to anterior border of valve.

TYPE MATERIAL: Chapman's type material which was used for the above description consists of three specimens, one complete valve and one dorsal and one ventral valve, each obtained from different depths of Mallee Bore No. 11. The holotype P12460 (length 5.5 mm, breadth 5 mm, depth 2 mm) was obtained from 160.2-161.54 m (525-530 ft), paratype P12461 (dorsal valve) from 46.93-48.15 m (154-158 ft) and paratype P12462 (ventral valve) from 34.74-45.72 m (114-150 ft). Numbers prefixed 'P' are in the Palaeontological Collection of the National Museum of Victoria.

STRATIGRAPHIC RANGE: Janjukian-Kalimnan.

OCCURRENCE: *South Australia:* *Morgan Limestone* (Balcombian): Between Morgan and Mannum, Murray River. *Dry Creek Sands* (Yatalan): Abattoirs Bore, Adelaide.

Victoria: *Point Addis Limestone* (Janjukian): Aireys Inlet. *Puebla Formation* (Longfordian): Torquay. *Fyansford Formation:* North Belmont Quarry (Batesfordian); Geelong (Bairnsdalian); Warrambine Creek, near Inverleigh (Bairnsdalian). *Muddy Creek Formation* (Balcombian): Clifton Bank, Muddy Creek, Hamilton. *Gippsland Limestone* (Bairnsdalian): Orbost Railway Cutting. *Gambier Limestone* (Bairnsdalian): Portland. *Sandringham Sands-Brighton Group* (Cheltenhamian) Beaumaris. *Bookpurnong Beds* (Cheltenhamian-Kalimnan): Mallee Bores No. 6 34.74-45.72 m (114-150 ft); 46.93-48.15 m (154-158 ft); No. 9 49.68-83.21 m (163-273 ft); No. 10 77.41-90.22 m (254-296 ft); 94.5-97.55 m (310-320 ft); No. 11 153.92-155.28 m (505-510 ft); 156.97-158.49 m (515-520 ft); 160.2-161.54 m (525-530 ft); 153.92-158.49 m (505-520 ft); 166.11-167.60 m (545-550 ft).

COMMENTS: The holotype (5.5 mm) is smaller in size than the largest specimens (9 mm) obtained from other localities cited above. In addition to the type material, Chapman's Collection of *M. portlandica* is represented in many other Mallee Bores but by only one or two specimens which are rarely complete. Sufficient material from which to gain some idea of the range of variation of the species was obtained from the Abattoirs Bore and Torquay. Features displaying variation are: anterior sulcation (moderate to pronounced), adductor muscle scar impressions (slight to deep) and the extent of the area between the socket ridges occupied by the cardinal process (one half to almost the total length of the socket ridges). In addition the median septum may taper off abruptly posteriorly or it may continue

as a low ridge to a point just beyond the posterior limits of the adductor muscle scars.

Ncobouchardia Thomson 1927

Neobouchardia Thomson 1927, *N.Z. Board Sci. & Art. Manual* No. 7: 270-1.

Neobouchardia Allan 1940, *Rec. Canterbury Mus.* 4 (6): 284-5.

Neobouchardia Hatai 1965, *Treatise on Invertebrate Paleontology*, H849.

TYPE SPECIES: (Original Designation) *Bouchardia minima* Thomson 1918.

STRATIGRAPHIC RANGE: Oligocene-Lower Miocene.

DISTRIBUTION: New Zealand (Oligocene-L. Miocene), Australia (Oligocene-L. Miocene).

DIAGNOSIS: Bouchardiinae with a minute epithyrid foramen and fused deltidial plates not delimited within the palintrope; with the cardinalia fused into a solid platform which displays three shallow caves anteriorly and a cardinal process with indented anterior rim; with a small, swollen boss on the septum.

Ncobouchardia minima (Thomson 1918)

(Pl. 7, fig. 7)

Bouchardia minima Thomson 1918, *Geol. Mag.* Dec. 6 (5): 260-1, figs. 1a-c.

Bouchardia minima Thomson 1920, *Trans. N.Z. Inst.* 52: 369.

Neobouchardia minima Thomson 1927, *N.Z. Board Sci. & Art. Manual* No. 7: 270-1, figs. 89a-c.

Neobouchardia minima Allan 1932, *Trans. N.Z. Inst.* 63 (1): 16.

Neobouchardia minima Allan 1940, *Rec. Canterbury Mus.* 4 (6): 285.

COMMENTS: Thomson's description (1927, p. 270-1) of the New Zealand members of this species is accurate for specimens found in each of the Australian localities cited below. As Allan (1940, p. 285) states: 'I am unable to separate the Victorian specimens from New Zealand topotypes. I reached this decision reluctantly after a careful comparison of external and internal details, because earlier records of Tertiary brachiopods common to both sides of the Tasman have not hitherto survived critical investigation'. Allan's Victorian specimens were collected from the Scutellina Limestone at Torquay, then the only known locality of *N. minima*.

A considerable effort has been made to find and dissect early ontogenetic stages of *N. minima* in order to display the nature of the hinge platform before excessive thickening of the posterior segment of the shell has taken place. The smallest sizes preserved ranged between 3-4 mm in length and all displayed considerable secondary thickening and a hinge platform of adult pattern.

OCCURRENCE: *New Zealand*: Kakanui Limestone (Lower Oligocene); Flat Top Hill; Oamaru, London Creek. *Main Mount Brown Limestone* (Upper Oligo-

cene to Miocene): Middle Waipara and Weka Pass District, Canterbury (type locality).

Victoria: Point Addis Limestone (Janjukian): Aireys Inlet. *Jan Juc Formation* (Janjukian): Marl below Point Addis Limestone, Bells Headland, Torquay. '*Scutellina Limestone*' (Longfordian); Jan Juc, Torquay.

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I wish to thank the Director and Staff of the National Museum of Victoria for providing the facilities to work with the Collections in their care and the additional help of Mr. T. A. Darragh in the preparation of the manuscript and the provision of stratigraphical data. Mr. George Kendrick of the Western Australian Museum supplied topotype material. Mr. Frank Guy of the Royal Melbourne Institute of Technology took the photographs, the cost of which was covered by a grant from the CSIRO Science and Industry Endowment Fund.

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DESCRIPTION OF PLATE 7

All photographs at a magnification of $\times 8$

- FIG. 1—*Malleia portlandica* (Chapman), P12460, holotype. Mallee Bore, No. 11, S.A.
FIG. 2—*Malleia portlandica* (Chapman), P12461, paratype, dorsal valve interior.
FIG. 3—*Malleia portlandica* (Chapman), P12462, paratype, ventral valve interior.
FIG. 4—*Malleia portlandica* (Chapman), P12460, holotype, anterior view.
FIG. 5—*Malleia portlandica* (Chapman), P30779, dorsal valve interior showing septal lamellae, Torquay, Victoria.
FIG. 6—*Malleia portlandica* (Chapman), P30780, dorsal valve interior, Abattoirs Bore, Adelaide, S.A.
FIG. 7—*Neobouchardia minima* (Thomson) P30781, dorsal valve interior, Torquay, Victoria.
Abbreviations: A = Adductor muscle scar, B = Posterior rim of cardinal process, C = Anterior rim of cardinal process.
FIG. 8—*Bouchardia rosea* (Mawe) F27471, dorsal valve interior, Rio de Janiero, South America.
Abbreviations: B = Posterior rim of cardinal process, C = Anterior rim of cardinal process.



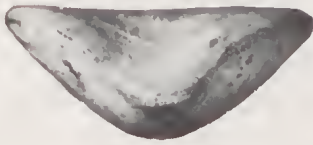
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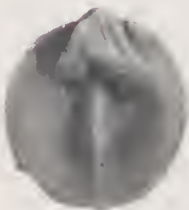
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SECOND LIST OF RADIOCARBON DATES ON SAMPLES FROM VICTORIA, AUSTRALIA

By EDMUND D. GILL*

A list of all radiocarbon dates on Victorian samples then available was published previously (Gill 1971). By request a second list is now published. The compiler is grateful to some researchers who have made dates available before they used them themselves. Some dates would never become available if it were not for lists of this kind. The format is that of the first list, and the date numbers follow on seriatim. The numbers provide the simplest mechanism for referring to a given date. As before, the list begins with the youngest and ends with the oldest. All dates are BP.

110. 220 ± 80 y (GaK-3521). Marine shells from Aboriginal midden in small tafoni cave in arkosc, NE. corner of 7.5 m terrace, small point on W. side of Point Sturt, Otway coast, Victoria. Coll. E. D. Gill. Provides age of occupation, and minimal age of tafoni formation.

111. 335 ± 50 y (N-834). Marine shells from Aboriginal midden in gray loam in Holocene dune at Ocean Grove, via Geelong, Victoria (Charcoal 1470 y). Coll. G. E. Williams. Gill et al. 1972.

112. 360 ± 105 y (N-517-2). A series of dates was obtained from Lake Keilambete, a maar 3.3 km NW. of Terang, Western Victoria. This date was on the inorganic part of sample LK4/11. Polach et al. 1970. Bowler and Hamada 1971.

113. 410 ± 70 y (GaK-3919). Marine shells from high energy shell grit/basalt boulder deposit forming vegetated terrace between vegetated dune and present shell grit beach. W. side of Horseshoe Bay and E. of Cape Reamur, 8 km W. of Port Fairy, Western Victoria. Gill 1973a.

114. 470 ± 105 y (N-832). Charcoal from Aboriginal midden in upper gray loam c. 1 m thick (approx. 7 m above basal dating of 5780 y) in dune at Ocean Grove, via Geelong, Victoria. Associated shells 335 ± 90 y. Coll. G. E. Williams. Gill et al. 1972.

115. 610 ± 110 y (N-517). Lake Keilambete sediments, Core 4, 11-21 cm. Bowler and Hamada 1971.

116. 935 ± 110 y (N-518). Lake Keilambete sediments, Core 4, 21-33 cm. Bowler and Hamada 1971.

117. 1040 ± 80 y (SUA-90). Marine shells from Aboriginal midden in juvenile soil on sand ridge overlying boulder bed with marine shells at mouth of Browns Creek behind beach, Otway coast, Victoria. Coll. E. D. Gill.

118. 1320 ± 80 y (SUA-87). Opercula of marine mollusc *Subnina undulata* from Aboriginal midden on Last Interglacial aeolianite cliff top, McKechnies Craigs, c. 1.3 km NW. of Cape Reamur, W. Vict., $38^{\circ} 23' S$, $142^{\circ} 8' E$. Port Fairy Military Map 091 671. Coll. E. D. Gill.

119. 1670 ± 90 y (GaK-2860). Fibrous peat from auger hole 1, 1.2-1.5 m, at Goose Lagoon. S. side of Princes Highway, 8 km west of Port Fairy, Victoria. Gill et al. 1972.

120. 1890 ± 115 y (N-390). Tree submerged by waters of Lake Keilambete and overlain by lacustrine sediments. Bowler and Hamada 1971.

121. 1970 ± 110 y (N-519). Lake Keilambete sediments. Core 4, 55-65 cm. Bowler and Hamada 1971.

122. 2015 ± 65 y (ANU-126). Carbonate nodules from Keilor terrace near Green Gully, c. 1 km S. of Keilor ($37^{\circ} 45' S$, $144^{\circ} 50' E$), Victoria. Bowler and Polach 1971.

123. 2020 ± 90 y (GaK-3215). Soil from upper terrace on NE. shore of Lake Corangamite, c. 0.5 km W. of prominent road cutting, North Cundare, via Colac, Western Victoria. Coll. E. D. Gill.

124. 2260 ± 90 y (GaK-3522). Fibrous peat from band 0.7-2.6 m at Goose Lagoon, S. side of Princes Highway, 8 km W. of Port Fairy, Western Victoria. Site in middle of swampy area crossed by the highway, and 4.6 m S. of its south boundary. Coll. E. D. Gill.

125. 2410 ± 120 y (N-520-1). Lake Keilambete sediments, Core 4, 79-90 cm. Bowler and Hamada 1971.

126. 2510 ± 110 y (GaK-2857). Marine shells from Aboriginal midden c. 0.2 km W. of Thunder Point Trigonometrical Station at Levy Point, in soil on Holocene sand overlying Last Interglacial aeolianite, c. 7 m above the sea. Gill et al. 1972.

127. 2530 ± 80 y (ANU-290). Carbonate from red-brown earth on Shepparton prior stream, NE. Vict. 0.75-1.50 m. Bowler and Polach 1971.

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128. **2560 \pm 120 y (N-520-2).** Lake Keilambete, inorganic fraction of sample LK4/79. Bowler and Hamada 1971.
129. **2600 \pm 110 y (N-521-1).** Lake Keilambete sediments, Core 4, 1.02-1.12 m. Bowler and Hamada 1971.
130. **2620 \pm 80 y (SUA-89).** Limpet shells from Aboriginal midden on neck of Cape Reamur, Western Victoria. In juvenile soil on sand rise above Last Interglacial Port Fairy Calcarene. Coll. E. D. Gill.
131. **2670 \pm 70 y (ANU-134).** Massive carbonate concretion 1.80 m deep in profile of red-brown earth on prior stream sediments exposed in right bank of Goulburn River 4.8 km S. of Shepparton, NE. Victoria. Bowler and Polach 1971.
132. **2830 \pm 100 y (GaK-3524).** Marine shells of rock facies on top of abandoned cliff of Last Interglacial aeolianite fronted by c. 80 m width of sand ridges plus the present sandy beach with sand facies molluscs only, Venus Bay, Gippsland, Victoria, c. 0.5 km SE. of Five Mile Creek. Coll. E. D. Gill.
133. **2840 \pm 80 y (GaK-3917).** Shells from formation of shell grit and basalt boulders filling former shoreline channel at W. end of Ocean Drive, Port Fairy, Western Victoria. Gill 1973a.
134. **2900 \pm 120 y (N-521-2).** Lake Keilambete, inorganic fraction of sample LK4/102. Bowler and Hamada 1971.
135. **2970 \pm 120 y (N-522-1).** Lake Keilambete sediments, Bore 4, 1.30-1.40 m. Bowler and Hamada 1971.
136. **3080 \pm 80 y (SUA-88).** Limpet shells from Aboriginal midden in juvenile soil on beach ridge at Dura Bay (Gill 1973a) on W. side of debouchement of Goose Lagoon drain. Port Fairy Military Map 134 663, W. of Port Fairy, W. Victoria. Coll. E. D. Gill.
137. **3150 \pm 100 y (GaK-2410).** Peat in Trotters Swamp at reservoir near Anakie, Brisbane Ranges, Victoria, depth 0.3 m. Coll. D. H. Ashton and N. Scarlett.
138. **3320 \pm 100 y (GaK-2858).** Opercula of marine mollusc *Subnivalia undulata* from black soil in Holocene sand at former outlet of Goose Lagoon where the coast running N. from Cape Reamur changes direction NW. to Yambuk, Western Victoria. Gill et al. 1972.
139. **3550 \pm 80 y (GaK-3990).** Amorphous peat 0.6 m from surface on slope under subalpine heath at Echo Flat, Lake Mountain. Check on GaK-3469, 3470. Coll. D. H. Ashton and G. J. Hargreaves.
140. **3580 \pm 125 y (N-523-1).** Lake Keilambete sediments Core 4, 1.65-1.75 m. Bowler and Hamada 1971.
141. **3880 \pm 90 y (GaK-3918).** *Katelsia* shells from emerged stillwater marine sandy shell bed in sewerage excavations on E. side of James St., Port Fairy, Western Victoria, behind coastal dune at South Beach Caravan Park. Gill 1973a.
142. **3950 \pm 100 y (GaK-3470).** Amorphous peat 1.2 m from surface on slope under subalpine heath, Echo Flat, Lake Mountain. Coll. D. H. Ashton and G. J. Hargreaves.
143. **4040 \pm 120 y (GaK-3216).** *Coxiella* shells (brackish-water gasteropods) from low terrace of consolidated sediments on E. shore of Lake Corangamite, c. 0.5 km west of prominent road cutting, North Cundare, Western Victoria. Coll. E. D. Gill.
144. **4150 \pm 190 y (N-522-2).** Lake Keilambete, inorganic fraction of sample LK4/130. Bowler and Hamada 1971.
145. **4200 \pm 125 y (N-524-1).** Lake Keilambete sediments, Core 4, 1.90-2 m. Bowler and Hamada 1971.
146. **4590 \pm 90 y (GaK-2108).** Horseshoe Cr., Everton. 146° 34' E, 36° 26' S. A discontinuous more or less horizontal bed of charcoal fragments of variable size c. 2.5 m below surface of stream terrace. 20th Ann. Rep. Soil Conserv. Auth. Viet. 1970, p. 28.
147. **5250 \pm 135 y (N-525-1).** Lake Keilambete sediments, Core 4, 2.35-2.45 m. Bowler and Hamada 1971.
148. **5350 \pm 110 y (GaK-3820).** Organic matter from earliest black soil in dunes at Diamond Bay, near Portsea, Sorrento Peninsula. Coll. E. C. F. Bird. Gill et al. 1972.
149. **5380 \pm 160 y (GaK-3469).** Sphagnum peat 0.6 m from surface of bog at Echo Flat, Lake Mountain. Coll. D. H. Ashton and G. J. Hargreaves.
150. **5430 \pm 135 y (N-523-2).** Lake Keilambete. Inorganic fraction of sample LK4/165. Bowler and Hamada 1971.
151. **5860 \pm 60 y (N-525-2).** Lake Keilambete. Inorganic fraction of sample LK4/235. Bowler and Hamada 1971.
152. **5780 \pm 140 y (N-831).** Charcoal from gray loam c. 1 m thick at base of Holocene dune, Ocean Grove, Central Victoria, overlying calcareous reddish sand. Coll. G. E. Williams. Gill et al. 1972.
153. **5790 \pm 95 y (ANU-181).** Fine-earth carbonate, 10 cm deep, from soil profile in quarry S. of Quambatook, 8 km W. of Kerang, North Victoria. Bowler and Polach 1971.
154. **5960 \pm 140 y (N-524-2).** Lake Keilambete. Inorganic fraction of sample LK4/190. Bowler and Hamada 1971.
155. **6260 \pm 100 y (ANU-291).** Carbonate from red-brown earth, 60-76 cm, prior stream, Echuca South, North Victoria. Bowler and Polach 1971.
156. **6290 \pm 140 y (N-526-2).** Lake Keilambete. Inorganic fraction of sample LK4/290. Bowler and Hamada 1971.
157. **6360 \pm 140 y (GaK-2416).** Five shells of the marine stillwater pelecypod *Anadara trapezia* from Davis shell Works, SW corner of Salt Lake, Sections 27-28 Parish of Paywit, County of Grant, Victoria. Gill et al 1971.
158. **6440 \pm 145 y (N-526-1).** Lake Keilambete

sediments, Core 4, 2.90-3 m. Bowler and Hamada 1971.

159. 6700 ± 90 y (ANU-135). Carbonate concretion from gravel pit in bed of prior stream of Campaspe system 8.9 km NE. of Rochester, Northern Victoria. Coll. from B horizon 1.1 m deep in red-brown earth. Bowler and Polach 1971.

160. 6760 ± 110 y (GaK-3519). Shells of marine pelecypod *Anapella cycladea* from an emerged sandy shell bed at Shallow Inlet, E. Victoria. Coll. Miss Ann Smith. Gill et al. 1972.

161. 7110 ± 95 y (ANU-90). Carbonate from 20-30 cm red-brown earth, Echuca prior stream. Bowler and Polach 1971.

162. 7240 ± 140 y (GaK-3706). Peat from base of post-basaltic swamp and lake sequence resulting from ponding by the Mt. Napier ejectamenta at Buckley's Swamp, Par. Yatchaw West, sect X1 (2), c. 965 m E. of the W. boundary and c. 482 m north of the S. boundary. Coll. L. K. M. Elmore and dated by E. D. Gill.

163. 7300 ± 150 y (GaK-2856). Aboriginal midden shells (marine) within compacted sandy tuff on top of Last Interglacial aeolianite cliff and Last Glacial red soil on east side of Table Cave embayment between Thunder Point and Point Pickering, Warrnambool, Western Victoria. Gill 1972.

164. 7850 ± 165 y (N-527-1). Lake Keilambete sediments, Core 4, 3.25-3.45 m. Bowler and Hamada 1971.

165. 8700 ± 150 y (GaK-3920). Laminated mammillary calcite overlying amorphous calcitic hard pan of Last Glacial age, formed over Last Interglacial dune and marine bed at Moulden Quarry, Dennington, Western Victoria. Gill 1967, 1973b.

166. 8790 ± 170 y (GaK-3922). Solid calcrete forming a mass of rhizomorph-like concretions standing seaward of Last Glacial hardpan and rhizomorphs, but at a lower level (top 1.2 m above beach), W. side of Cape Reamur, Western Victoria. Gill 1973b.

167. 9860 ± 180 y (N-527-2). Lake Keilambete. Inorganic fraction of samples LK4/325. Bowler and Hamada 1971.

168. $10,060 \pm 140$ y (ANU-182). Quambatook Quarry (see 153) carbonate in calcareous red earth at 50-60 cm. Bowler and Polach 1971.

169. $14,200 \pm 790$ y (N.Z. R2729/1). Soil carbonate at 0.6-0.9 m from auger hole on crest of E.-W. dune on Berribee Station, SSW. of homestead, NW. Victoria. Gill 1973c.

170. $14,300 \pm 300$ y (N-528). Lake Keilambete sediments Core 4 at 3.95-4.12 m. Bowler and Hamada 1971.

171. $14,900 \pm 300$ y (N-835). Shells of marine gastropod *Subnina undulata* from beach rock at Ocean Grove, Victoria. Coll. G. E. Williams. Gill et al. 1972.

172. $15,220 \pm 530$ y (GaK-3214). Carbon from thin
— 320

uniform soil in prominent road cutting at North Cundare, E. side of Lake Corangamite, Western Victoria. (Above shell layer dated 28,240 y. See 102.) Coll. E. D. Gill.

173. $15,550 \pm 230$ y (ANU-183). Fine earth carbonate in B horizon 65 cm deep in highest soil unit (Kyalite) of Churchward. Bowler and Polach 1971.

174. $16,400 \pm 450$ y (GaK-3218). Carbonate from
— 560 paleosol in E.-W. dune N. of Ouyen on Calder Highway, Northern Victoria. Gill 1973c.

175. $20,340 \pm 500$ y (ANU-199). Lake Keilambete sediments. Carbonate from upper marl below discontinuity. Bowler and Hamada 1971.

176. $20,350 \pm 450$ y (GaK-3921). Calcrete rhizomorph from Port Fairy Calcarene (Last Interglacial) on coast on W. side of Cape Reamur, Western Victoria. Gill 1973b.

177. $21,600 \pm 650$ y (N-567). Lake Keilambete sediments, sample LK37. Inorganic carbon from highest of three marl bands. Bowler and Hamada 1971.

178. $24,000 \pm 900$ y (ANU 184). Porous nodular carbonate from second soil unit (Speewa) of Churchward, from dune at Nyah West, Northern Victoria. Bowler and Polach 1971.

179. $27,500 \pm 700$ y (N.Z. R2729/4). Soil nodules of calcite and quartz from base of E.-W. dune on E. side of Calder Highway S. of Hattah, Northern Victoria. Gill 1973c.

180. $28,000 \pm 1700$ y (GaK-3288). *Ostrea sinuata* from
— 1300 W. of Lake Melanyara from bottom of large drain beside road 1.6 km ENE. of Sale, E. Victoria. Military map reference 112,043. Coll. W. T. Ward. Average of eight U/Th assays by J. C. Schornick is 101,000 y. Gill et al. 1972.

181. $29,100 \pm 1250$ y (N-566). Lake Keilambete sediments, sample LK34. Inorganic carbon from lowest of three marl bands. Bowler and Hamada 1971.

182. $29,750 \pm 1450$ y (ANU-185). Porous nodular carbonate from lowest soil unit described by Churchward. Nyah West, Northern Victoria. Bowler and Polach 1971.

183. $30,700 \pm 2400$ y (GaK-3523). Worn marine shells
— 2000 from high energy marine deposit at base of aeolianite dune, 0.4 km N. of bridge over Hopkins River, Warrnambool, Western Victoria. U/Th shows older. Coll. E. D. Gill.

184. $> 34,300$ y (N.Z. R2729/3). Paleosol carbonate from 4.6-5.5 m in auger hole from crest of E.-W. dune on Berribee Station, SSW. of homestead, NE. Victoria. Gill 1973c.

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NOTHOFAGUS CUNNINGHAMII ECOTONAL STAGES Buried Viable Seed in North West Tasmania

By TRUDA M. HOWARD*

ABSTRACT: The buried viable seed from three vegetation types at West Downs, Surrey Hills, North West Tasmania, was germinated and species types and numbers recorded. The three vegetation types were a *Poa gunnii* dominated grassland, a closed *Nothofagus cunninghamii* forest and an *Acacia melanoxylon* dominated ecotone between these two, on a kraznozem derived from basalt at 1900 ft (579 m).

Of the seeds germinating from the soil, the numbers diminished with depth, woody species were poorly represented, and in the two forest soils, grasses, rushes, sedges and herbs not present in the vegetation were abundant.

Difference between the species composition of the stored seed and the present vegetation were found to correlate with seral stages observed after burning or logging of forests in the Surrey Hills district.

INTRODUCTION

Observations made on the viable seed stored in a successional series of old field and forest soils by Oosting and Humphreys (1940) led them to the conclusions that viable seeds in the soil undergo succession as do the plants above ground. They also found that viable buried seed can to some extent indicate the probable species present in the next successional stage. Howard and Ashton (1967) studied the viable seed stored under burnt and unburnt *Eucalyptus pauciflora* subalpine woodland at Lake Mountain, Victoria, and came to the conclusion that such seed may be as important as the current seed crop in determining the composition of regenerating vegetation after fire.

In this investigation, the species composition of the buried viable seed in three vegetation types at West Downs (Surrey Hills, North West Tasmania) was determined, and the results related to the mosaic of communities observed in the area. Fires have played an important part in producing this mosaic, and it was hoped that buried viable seed could provide further evidence for the successional status of some vegetation types.

GENERAL ENVIRONMENT

West Downs is located in the Surrey Hills, approximately 20 miles (32 km) south of Burnie,

Tasmania. The area under study has a general elevation of 1900 ft (579 m), and is on the western boundary of an extensive Tertiary basalt plateau, which drops away sharply to the Hellyer River. Soils in the area are predominantly kraznozems (Stephens, 1962). The rainfall of the area is reliable and probably exceeds 70 in (177 cm) p.a. Snow may occur in winter, but rarely persists for more than a week. The summers are mild, and the winters very cool, frosts may occur throughout the year, and in winter minima of -10°C are not uncommon.

The area under study (Fig. 1) consists of a small, shortly turfed grass plain surrounded on the north by mature *Nothofagus cunninghamii* closed forest (Specht, 1970), on the east by mature and on the west by young mixed tall open eucalypt forest/closed *Nothofagus* forest. The boundary between the grassland and closed *Nothofagus* forest is extremely abrupt, whereas the boundary between the western edge of the grassland and the young tall open forest/closed forest is extensive, and a number of different phases can be recognized. Within one of these phases (dominated by *Acacia melanoxylon*) sampling for soil seed estimates was carried out.

STAND DESCRIPTIONS

(1) Closed *Nothofagus cunninghamii* forest.

This stand (Fig. 1, V) consists of uneven aged

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Nothofagus cunninghamii and *Atherosperma moschatum* trees up to 120 ft (36.5 m) in height, with a combined crown cover of more than 75%. The understorey is sparse (less than 10% cover) but can be divided into a tall shrub (15-20 ft, 4.5-6 m) layer, mainly of *Drimys lanceolata* with occasional *Cenarrhenes nitida* bushes, and a diffuse tree fern stratum (8 ft, 2.4 m) dominated by *Dicksonia antarctica*. Ground cover by ferns (especially *Polystichum proliferum*) is very patchy. Grasses and herbs are absent, but mosses, lichens and liverworts are abundant on tree trunks, large branches and fallen logs, but only locally abundant on the soil. A litter layer of 1-2 in (2.5-5.0 cms) is well developed over the remainder of the forest floor, and may be up

to one foot deep around the boles of old *Nothofagus* trees.

This stand has probably been stable as closed *Nothofagus* forest for the last 400 years at least, and may have been undisturbed by external influences for 800 years or more (Howard, 1973a).

(2) Grassland

The grassland (Fig. 1, I) is dominated by *Poa gunnii* with *Agropyron pectinatum* locally abundant. Grass cover is continuous except for occasional hollows, which are waterfilled in winter, where a thin cover of *Polystichum* spp. is present. In the short springy turf numerous herb species occur, the most abundant being *Viola hederacea*, *V. betonicifolia*, *Gnaphalium collinum*, *Oxalis corniculata*, *Hydrocotyle sibthorpioides*, *Diurus pedunculata* and *Luzula campestris*. The moss *Thuidium furfursum* var. *sparsum* is present throughout the turf, while the surface of the turf is dusted with individuals of *Cladia retipora*. Three shrub species are abundant throughout the grassland, *Lissanthe montana* (1 ft, 0.3 m), *Hakea microcarpa* which forms local thickets up to 10 ft (3.4 m) and *Drimys lanceolata* as individual shrubs up to 25 ft (7.6 m) tall.

It is probable that some at least of this grassy plain has been stable for a long time, as there is no evidence of tree charcoal and few irregularities in the plain surface which can be related to those within the closed *Nothofagus* forest. The presence of very narrow charcoal bands in the soil suggest that the plain has been maintained by fire, and the existence of a complex ecotone on the west shows that the plain may fluctuate in size.

(3) The Ecotone

Passing from the grassland to the tall open eucalypt/closed forest, various zones in the ecotone may be characterized as:

(a) *Poa gunnii* and *Pteridium esculentum* equally abundant (included in III in Fig. 1).

(b) *Pteridium esculentum* dominant, *Poa gunnii* almost absent, *Drimys lanceolata* tall (15-25 ft, 4.5-7.6 m) shrubs very abundant (included in III in Fig. 1).

(c) *Pteridium esculentum* almost entirely replaced by *Histiopteris incisa*, ground cover absent in many places; *Drimys lanceolata* present as tall straggling shrubs (20-30 ft, 6-9 m) irregularly distributed under a tree stratum (70-80 ft, 21.3-24.3 m) of *Acacia melanoxylon*; ground-ferns and tree ferns abundant (II in Fig. 1).

Sampling was carried out in the last described zone. *Acacia melanoxylon* occurs as very large mature trees, carrying a rich flora of epiphytic mosses and lichens, a few liverworts and abundant

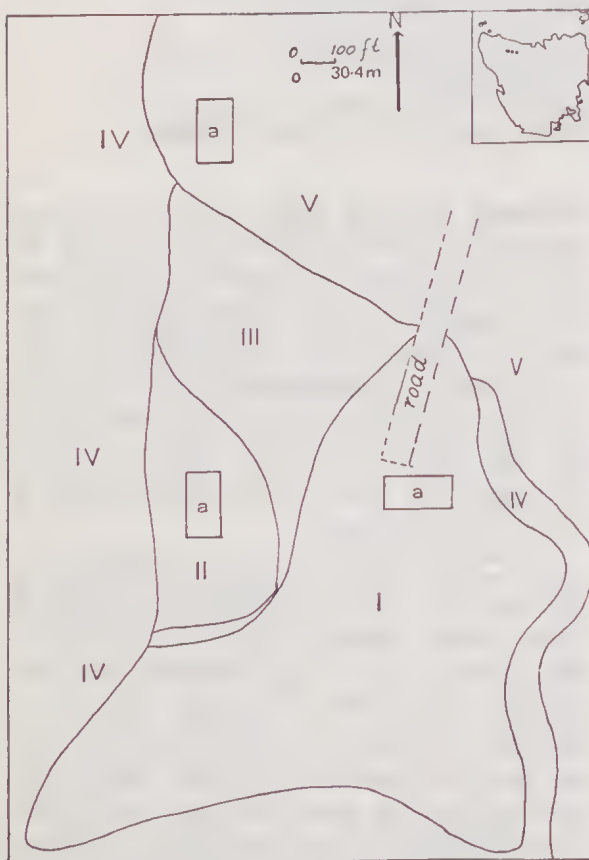


FIG. 1.—West Downs plain and surrounding vegetation, to show sample sites. The inset of Tasmania shows the location of the Surrey Hills. I. *Poa gunnii*—*Hakea microcarpa*. II. *Drimys lanceolata*—*Acacia melanoxylon*. III. *Poa gunnii*—*Drimys lanceolata*—*Pteridium esculentum*. IV. *Eucalyptus delegatensis*—*Atherosperma moschatum*—*Nothofagus cunninghamii*. V. *Nothofagus cunninghamii*—*Atherosperma moschatum*. □ Areas within which soil-seed samples were collected.

Microsorium diversifolium on main branches and trunks. Lichens and mosses (especially *Dicranoloma meuziesii*) are abundant on the forest floor, over an aromatic litter layer 1-2 in (25-50 mm) deep. The total crown cover is high (more than 85%), so that this forest is even darker than the closed *Nothofagus* forest.

METHODS

Soil was carefully excavated from five random sites, each measuring 12 x 12 in (300 x 300 mm) in each stand in August 1970. One inch deep slices of soil were collected for each replicate at 0-1 in, 1-2 in, 3-4 in and 5-6 in (25 mm, 25-50 mm, 75-100 mm, 125-150 mm). All samples were sieved in a laboratory to remove roots, corms, tubers, rhizomes and rock and were spread evenly in 12 x 12 x 2 in (300 x 300 x 50 mm) plastic trays. For both closed *Nothofagus* and *Acacia melanoxylon* forest, soils from 0-1 in (25 mm) and 1-2 in (25-50 mm) were shallow in the trays due to the high proportion of roots in these samples. This was particularly marked for the *A. melanoxylon* soil where more than half these samples was a mat of tree roots. The trays were placed in a glasshouse, and kept uniformly moist.

All seedlings were identified, counted and removed as they appeared. After about four months the main flush of germination had passed, and the soil was turned over. As very little further germination occurred after one year, the majority of replicates was discarded at this time.

At the time of soil collection, all species present in the vicinity (c. 100 ft, 30 m) of the sample sites were recorded, and their cover class estimated.

RESULTS

In Tables 1-3 the species germinating from each vegetation type and depth are shown in comparison with the angiosperm species present as living plants. After five to six months in the glasshouse both the *Nothofagus* and *A. melanoxylon* forest soils developed a dense cover of *Histiopteris incisa* and *Hypolepis australis*. Both these ferns occur in the present *A. melanoxylon* stand, but are absent from the *Nothofagus* forest. No tree fern or *Polystichum proliferum* plants developed. Some mosses developed on all soil samples but these were most abundant on the grassland soil, where *Polytrichum* sp. was very abundant. A few ferns developed from the grass-

TABLE 1

SPECIES COMPOSITION (ANGIOSPERMS) OF THE CLOSED *Nothofagus cunninghamii* FOREST COMPARED WITH THE SPECIES GERMINATING FROM THE SOIL AT EACH SAMPLE DEPTH. SPECIES NAMES FOLLOW CURTIS (1956-1967) AND WILLIS (1962).

Species	Stand*	Density of germinable seed per square foot			
		0-1", 25 mm	1-2", 25-50 mm	3-4", 75-100 mm	5-6", 125-150 mm
<i>Drimys lanceolata</i>	2	4.6	2.4	0.6	0.8
<i>Acacia melanoxylon</i>			0.2		
<i>Coprosma quadrifida</i>	1				
<i>Gaultheria hispidula</i>				0.2	
<i>Pittosporum bicolor</i>	†		0.2		
<i>Cenarrhenes nitida</i>	†				
<i>Phyllocladus aspleniifolius</i>	†				
<i>Atherosperma moschatum</i>	3				
<i>Nothofagus cunninghamii</i>	5		0.2		
<i>Zieria arborescens</i>			0.2	0.2	
<i>Libertia pulchella</i>	1				
<i>Luzula campestris</i>	†	1.2	3.0	3.0	1.2
<i>Agropyron pectinatum</i>		0.2			
<i>Juncus</i> sp.		0.6	0.8	0.2	1.0
<i>Poa gunnii</i>		0.6	1.6	2.6	0.4
<i>Carex</i> sp.			0.6		
<i>Hydrocotyle sibthorpioides</i>			0.4	0.8	0.6
<i>Acaena auaseriifolia</i>		0.4	1.4		
<i>Viola hederacea</i>			0.6	0.2	
<i>Gnaphalium collinum</i>		0.2			
<i>Hypericum japonicum</i>		0.2	1.4	1.6	1.8
<i>Cotula filicula</i>				0.2	
Total		8.4	12.6	9.6	6.0
% Woody Species		59.5	22.2	42.0	13.3

* Cover rating for species in existing stands—†, less 1%, 1, 1-5%, 2, 5-25%, 3, 25-50%, 4, 50-75%, 5, 75-100%.

land 0-25 mm samples only. *Marchantia* sp. thalli appeared on the *Nothofagus* and *A. melanoxylon* soils.

The main points illustrated by Tables 1-3 are:
 (a) The number of germinable seeds stored in the soil generally diminishes with sample depth.
 (b) The smallest number of seeds was stored in the *Nothofagus cunninghamii* closed forest soil.
 (c) None of the woody species present in the grassland germinated from grassland soils.
 (d) Grasses, rushes, sedges and herbs, though largely absent from both *Nothofagus* and *Acacia melanoxylon* stands were well represented as seeds in these forest soils.

Of particular interest is the presence of *Acacia melanoxylon* seed in the *Nothofagus* forest soil although trees of this species are absent from the stand.

The majority of species germinated in the first six months after the soil was placed in the glass-house, although the majority of *Drimys lanceolata* seedlings did not appear until the following spring.

DISCUSSION

The closed *Nothofagus* forest germination, 21 seedlings per 12 x 12 x 2 in (300 x 300 x 50 mm) is low when compared with the figure for a similar forest at Cement Creek, Victoria (120

seedlings per 12 x 12 x 2 in (300 x 300 x 50 mm) Carrol & Ashton, 1965). This may be a reflection of both the less diverse flora of the West Downs stand and of the greater age of the forest. The presence of herb, rush, grass and sedge species in the *Nothofagus* forest soil either reflects the longevity of some of these seeds (rush and sedge), or the ease with which they can be introduced from surrounding vegetation types (grass and herb).

The germinable seed present in the top two inches of the grassland soil (173) also appears to be low when compared with other grassy areas (e.g. red gum woodland, Yan Yean, 2303, Howard & Ashton, 1967). This may be due in part to the density of the sward (which was removed before soil collection) impeding seed penetration into the soil. Very heavy grazing of flowering grass heads by wallabies (*Macropus rufogriseus*) and wombats (*Vombatus ursinus*), may also be a contributing factor. Although woody perennials in general are often under represented by buried viable seed, the failure of any shrub species to germinate from this soil may be attributed to a different factor for each species. The fleshy fruits of *Lissanthe montana* are eaten as soon as they ripen, the hard follicles of *Hakea microcarpa* do not usually release viable seed

TABLE 2

SPECIES COMPOSITION (ANGIOSPERMS) OF THE CLOSED *Acacia melanoxylon* STAND COMPARED WITH THE SPECIES GERMINATING FROM THE SOIL AT EACH SAMPLE DEPTH.

Species	Stand*	Density of germinable seed per square foot			
		0-1", 25 mm	1-2", 25-50 mm	3-4", 75-100 mm	5-6", 125-150 mm
<i>Drimys lanceolata</i>	†	6.4			
<i>Acacia melanoxylon</i>	5	1.4		0.8	
<i>Coprosma quadrifida</i>	†	3.0		0.4	
<i>Gaultheria hispida</i>			1.6		0.2
<i>Pittosporum bicolor</i>	†	0.2			
<i>Luzula campestris</i>		5.0	13.2	8.6	5.4
<i>Agropyron pectinatum</i>		2.0	2.6	2.8	
<i>Juncus</i> sp.		0.6	1.4	2.4	0.2
<i>Poa gunnii</i>		0.6	0.4	2.4	0.4
<i>Carex</i> sp.		4.4	8.8	15.6	6.4
<i>Hydrocotyle sibthorpioides</i>	†	46.4	48.8	35.8	16.2
<i>Acaena anserinifolia</i>	†	0.2	0.8		
<i>Geranium microphyllum</i>	†	0.4	0.4		
<i>Oxalis corniculata</i>	†	29.0	21.0	24.2	7.2
<i>Australina pusilla</i>	†	3.8	8.0	4.6	2.0
<i>Cardamine intermedia</i>	†	1.6	0.4	0.2	
<i>Viola hederacea</i>		0.8	2.0	1.4	1.4
<i>Gnaphalium collinum</i>		0.2	0.2		
<i>Hypericum japonicum</i>		1.2	1.2	4.0	1.6
<i>Lagenophora stipitata</i>		0.2	0.6	0.6	0.2
<i>Centaureum erythraea</i>			0.4	0.4	0.2
Total		107.4	111.8	103.2	41.4
% Woody Species		10.2	1.4	1.2	1.4

*See Table 1.

without the intervention of fire, and the seeds of *Drimys lanceolata* are extensively harvested by ants which live only in the grassland.

The seed stored in the soil of the *Acacia melanoxylon* forest (220 seeds per 12 x 12 x 2 in, 300 x 300 x 50 mm) is greater than for either grassland or *Nothofagus* forest. More than a third of this seed is of *Hydrocotyle sibthorpioides*, which is poorly represented in the vegetation at present.

The failure of most *Drimys lanceolata* seeds to germinate until a year after soil collection suggests that the abundant autumn 1970 crop had to undergo some 'pre-treatment' before it would germinate. Experiments with washing seeds, and the observation that seeds sometimes germinate on the shrubs after prolonged heavy rain suggests that there is a water soluble inhibitor involved in retarding seed germination.

The abundance of *Hydrocotyle sibthorpioides*, *Carex* sp., *Juncus* sp., and *Oxalis corniculata* in the *Acacia melanoxylon* forest soil support the supposition based on observation, that this stand is present as the result of burning. In the Surrey Hills district, when a *Nothofagus* or mixed *E. delegatensis*/*Nothofagus* forest is severely burnt,

the early stages of succession are usually marked by an abundance of rushes, sedges, *Hydrocotyle sibthorpioides*, *Oxalis corniculata* and *Marchantia* sp. on the ground, regardless of which species of trees and/or shrubs have established. This early phase is usually followed after 1-2 years by rushes, sedges and fern species (*Hypolepis australis*, *Histiopteris incisa*) dominating the understory. Should the tree or shrub stratum become sufficiently dense, all these species are suppressed and die. It appears, however, that these seeds and spores are stored for remarkably long periods in the soil. The *A. melanoxylon* stand in question has been present for at least 60 years, and the neighbouring *Nothofagus* forest, where *Carex* sp. and *Juncus* sp. still persist as seeds, is more than 400 years old. The presence of abundant *Carex* sp. seed in the grassland soil suggests that the grassland may also go through a phase, after fire, when this species is abundant before grass tussocks re-establish themselves.

Nothofagus cunninghamii, the dominant tree of the closed forest, was poorly represented amongst germinating seedlings from this forest soil. This is a reflection of the sampling time (August), as by this time of the year nearly all

TABLE 3

SPECIES COMPOSITION (ANGIOSPERMS) OF THE GRASSLAND, COMPARED WITH THE SPECIES GERMINATING FROM THE SOIL AT EACH SAMPLE DEPTH.

Species	Stand*	Density of germinable seed per square foot			
		0-1", 25 mm	1-2", 25-50 mm	3-4", 75-100 mm	5-6", 125-150 mm
<i>Hakea microcarpa</i>	2				
<i>Lissanthe montana</i>	1				
<i>Drimys lanceolata</i>	†				
<i>Luzula campestris</i>	†	17.0	8.8	4.2	2.4
<i>Agropyron pectinatum</i>	1	10.0	10.4	1.6	0.8
<i>Juncus</i> sp.		0.6	0.4	0.4	0.2
<i>Poa gunnii</i>	5	5.2	2.4	1.6	0.6
<i>Carex</i> sp.		17.2	14.6	4.4	2.4
<i>Prasophyllum suttonii</i>	†				
<i>Diurus peduncularis</i>	†	40.2	4.8	0.8	0.2
<i>Hydrocotyle sibthorpioides</i>	†	0.4	0.4	0.6	0.2
<i>Oxalis corniculata</i>	†	0.2			0.2
<i>Viola hederacea</i>	†	2.2	3.4	1.0	0.6
<i>Gnaphalium collinum</i>	†	0.2			
<i>Hypericum japonicum</i>	†	20.4	12.2	6.4	0.8
<i>Lagenophora stipitata</i>					0.2
<i>Centaureum erythraea</i>	†	1.6	2.2	0.4	
<i>Cotula filicula</i>	†				
<i>Viola betonicifolia</i>	†				
<i>Helichrysum scorpioides</i>	†				
<i>Craspedia glauca</i> var. <i>gracilis</i>	†				
<i>Leptorhynchos squamatus</i>	†				
<i>Brachycome diversifolia</i>	†				
<i>Oxalis lactea</i>	†				
Total		115.2	59.6	21.4	8.6
% Woody Species		0	0	0	0

*See Table 1.

seed has decayed or been destroyed (Howard, 1973b), and more will not fall until the following February. The *Acacia melanoxylon* seed which germinated from the 1-2 in layer of this soil has probably been stored for an extremely long period, as no *A. melanoxylon* trees are present in the stand now.

The seeds of both *Nothofagus cunninghamii* and *Acacia melanoxylon* are relatively bulky (5 x 3 mm), but *Acacia melanoxylon* seeds are much less likely to be transported by wind and insects, as they are 10 times heavier than those of *Nothofagus cunninghamii* (500/gm cf. 52/gm). This reinforces the supposition that the *Acacia melanoxylon* seed present in the mature *Nothofagus cunninghamii* stand has been stored in this soil, rather than transported to it.

The absence of *Atherosperma moschatum*, the sub-dominant species in this forest, may also be due to the sampling time, but for this species seed set is irregular, whereas for *Nothofagus cunninghamii* it is regular and abundant. It is possible to conclude that a severe fire through this forest at most times of the year would result in a tall shrub dominated regeneration stand (*Drimys lanceolata*) with occasional *A. melanoxylon* as emergent trees. Only during the time of *Nothofagus* seed fall is there much chance that a fire would be followed by the regeneration of a *Nothofagus* closed forest.

Acacia melanoxylon, which now dominates an ecotonal area between grassland and *Eucalyptus delegatensis*/*Nothofagus* forest has apparently been stabilized in this position by repeated fires which have prevented the re-establishment of eucalypts in the area. In other areas of West Downs the grassland abuts directly onto mixed *E. delegatensis*/*Nothofagus* forest without passing through a belt of *Acacia melanoxylon*. The re-establishment of an *E. delegatensis* dominated stand after one has been burnt, presupposes the existence of seed, either stored in the soil (poor supply usually), or in mature capsules in the tree crowns. Over most of Surrey Hills, *E. delegatensis* seed set is very irregular (up to four years may pass with no seed set (D. de Boer, pers. comm.)), and seed crops are often very light. It is not unreasonable to suppose, therefore, that the *A. melanoxylon* stand resulted originally from a fire (probably originating in the grassland) during a year in which no *E. delegatensis* seed was available, and that this fire burnt a short way into the mixed *E. delegatensis*/*Nothofagus* forest.

Although the mixed *E. delegatensis*/*Nothofagus* forest abutting the *Acacia melanoxylon*/*Drimys lanceolata* zone contains *Nothofagus* trees which

flower regularly, no seedlings of *Nothofagus* were found in the *Acacia melanoxylon* stand, though they were abundant in the mixed forest. The very heavy shade cast by the *Acacia melanoxylon* trees presumably prevents *Nothofagus* regeneration, so that this forest type may represent an alternative climax form. It is quite probable that as *Acacia melanoxylon* trees die, they will be replaced by *Nothofagus* seedlings, thus the formation of a closed *A. melanoxylon* canopy may be only a temporary check in the succession to closed *Nothofagus* forest.

From these observations of the present vegetation, and viable soil stored seed, it has been possible to make some deductions about the past history of the vegetation and its possible future should a catastrophe such as fire occur. When such predictions are combined with observations of suspected seral stages in the Surrey Hills district, these stages become easier to interpret. Thus it would appear that, in an area such as Surrey Hills, of reasonably uniform soil, climate and topography, a considerable amount of evidence can be gained from investigations of soil seed to support general hypotheses on the possible seral relationships between observed vegetation types.

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STRATIGRAPHIC AND ISOTOPIC AGES OF TERTIARY BASALTS AT MAUDE AND AIREYS INLET, VICTORIA, AUSTRALIA

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ABSTRACT: Tertiary basalts at Maude and Aireys Inlet, Victoria, have been dated on the basis of foraminiferal and stratigraphic evidence and K-Ar determinations. The Maude Basalt, between two fossiliferous marine limestones, is shown to be early Longfordian (very early Miocene) in age and has been dated by the K-Ar method as 21.4 m.y. Another basalt, overlain by marine limestone, at Aireys Inlet is stratigraphically older than late Janjukian (late Oligocene) and has been isotopically dated as 26.5 to 27 m.y. The implications of these results in respect to local correlation, stages and foraminiferal zones, as well as agreement with the intercontinentally applied time scale, are discussed.

MAUDE BASALT

STRATIGRAPHIC RELATIONS AND AGE

In the vicinity of Maude (Figs. 1 and 2) and for about 10 km to the southeast the Maude Basalt (23 m thick at Maude; up to about 30 m thick elsewhere) overlies the Lower Maude Limestone Member of the Lower Maude Formation, and is in turn overlain by the Upper Maude Limestone (stratigraphic nomenclature after Bowler, 1963). The relationship between the basalt and the underlying limestone (Fig. 3) may be regarded as essentially conformable, although the contact is not well exposed; there is no evidence of notable erosion of the limestone, and the time interval between the cessation of limestone deposition and extrusion of the basalt is considered to have been negligible. The upper surface of the basalt is, in contrast, obviously eroded; pebbles of basalt are incorporated in basal beds of the Upper Maude Limestone and calcareous sediment fills deep crevices in the basalt.

The Lower Maude Limestone Member (9 m thick at Maude; up to 20 m thick elsewhere) contains a foraminiferal fauna in which planktonic specimens are very rare; benthonic species include *Sherbornina atkinsoni* Chapman, *Calcarina mackayi* (Karrer), *Astronion centroplax* Carter and *Amphistegina* sp. (Use of generic names in this paper follows common usage in fairly recent Australian literature; some of these

names have been lately revised or require revision). In terms of informal numbered zones based on Carter's (1958a, b, etc.) 'Faunal Units', the Lower Maude Limestone Member most probably represents zone 5, although *Victoriella conoidea* (Rutten), characteristically present in this zone, has not been observed in the limestone; possibly the upper strata of the member extend into zone 6. Thus in terms of southeastern Australian stages, used here in the redefined sense of Carter (1959), the Lower Maude Limestone Member is late Janjukian, possibly in part very early Longfordian, in age.

The numbered zones used here are regarded as informal regional time-rock (i.e. chronostratigraphic) units or approximating such as far as can be ascertained. Other workers, e.g. Wade (1964), Taylor (1966), Ludbrook and Lindsay (1969), have proposed different schemes of zonation and zonal nomenclature for application in southeastern Australia. These different schemes have been compared with each other (and with Carter's 'Faunal Units' and zones) and correlated with the internationally recognized sequence of P- and N- zones, based essentially on tropical planktonic foraminiferal associations, by McGowan et al. (1971). A single scheme of formally named Tertiary foraminiferal zones is not at present widely accepted in Australia.

In the vicinity of Maude, basal beds of the Upper Maude Limestone (12 m thick at Maude,

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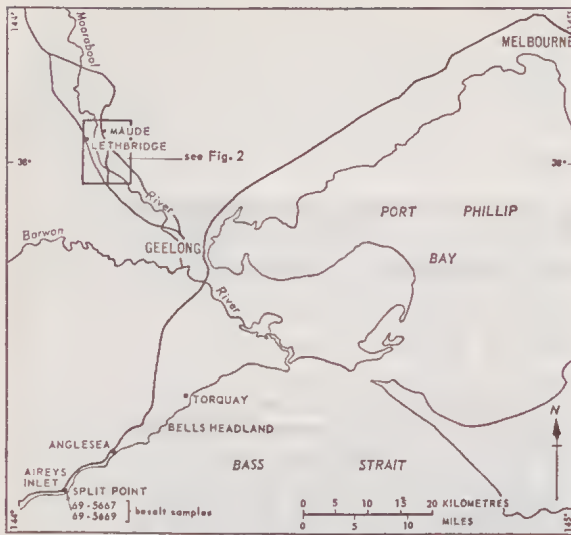


FIG. 1—Locality map.

thinner elsewhere) contain sparse foraminiferal assemblages. Wade and Carter (1957) recorded the presence of both *Sherbornina atkinsoni* and *S. cuneimarginata* Wade at the base of the limestone at Maude (locality F1 in Fig. 2, where Bowler's section 15 is exposed), whereas Bowler (1963) reported *Lepidocyclina* and *Gypsina howchini* Chapman from strata immediately overlying the Maude Basalt at this locality. None of these species has been observed in the basal beds of the formation at Maude by the present writers; however, *S. cuneimarginata* and *Planorbulinella plana* (Heron-Allen and Earland) have been noted at a higher stratigraphic level in the Upper Maude Limestone (just below Bowler's bed 'C'). To the south and south-southeast of Maude *Globigerinoides trilobus trilobus* (Reuss) is present at or very near the base of the limestone in some sections, e.g. at localities F3 (near Bowler's section 13), F6 and other exposures further southeast of Lowndes Bridge, while in other sections, e.g. F4 (= Bowler's section 12) and F5, both near 'The Pimple' hill, *G. trilobus* has not been observed in the lower 6 m of the formation, although other planktonic foraminifera, including rare *Globoquadrina dehiscens* (Chapman, Parr and Collins), are common. In sections at F2 (= Bowler's section 14), F4 and F6, *P. plana* and/or *Operculina victoriensis* Chapman and Parr are also present at or very near the base of the Upper Maude Limestone.

On the basis of the above evidence the Upper Maude Limestone in exposures south and south-southeast of Maude (i.e. in the vicinity of the localities from which samples of the Maude Basalt were collected for K-Ar dating) is regarded

as representing zones 6 to 7 and thus as early to mid-Longfordian in age. At Maude, the limestone represents a similar time interval on the evidence of both Wade and Carter (1957) and the writers' observations. Bowler's (1963) record of *Lepidocyclina*, indicating Batesfordian age, is not in agreement with the conclusions of other workers.

Apparently the unconformity at the top of the Maude Basalt represents a relatively short break in the continuity of deposition. The basalt is regarded as equivalent in age to zone 6, probably to its lower rather than upper part and perhaps even as approximating the boundary between zones 5 and 6. Thus the Maude Basalt is most probably very early Longfordian in age.

ISOTOPIC DATING

The isotopically dated whole rock samples of the Maude Basalt were collected at three localities up to 5 km apart (Fig. 2). The analytical methods and precision of argon and potassium determination in this study are the same as those reported by McDougall (1966) and Cooper (1963). The K-Ar results listed in Table 1 (a) are quite concordant and give a mean age of 21.4 ± 0.2 m.y., the error being one standard deviation of the mean (it is noted that this 21.4 m.y. age is slightly older than that referred to in Page and McDougall, 1970, due to a calibration adjust-

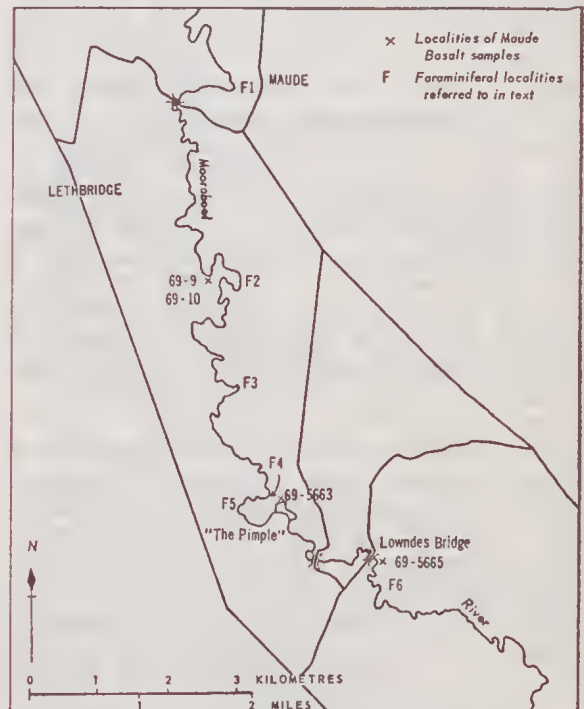


FIG. 2—Maude area locality map.

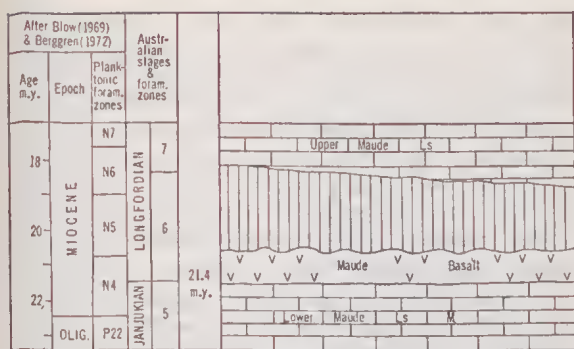


FIG. 3—Stratigraphic relationships in the vicinity of Maude.

ment). The errors quoted for individual ages are also one standard deviation as calculated from the uncertainties in the physical measurements. One of the results (69-9) has been duplicated to within experimental error and the average for the four samples of 21.4 ± 0.2 m.y. is regarded as a meaningful minimum age for the Maude Basalt.

DISCUSSION

The Oligocene-Miocene boundary is now generally equated, though not by all workers (e.g.

Eames, 1970), with the base of the Aquitanian Stage. In the type Aquitanian region of south-western France, the Aquitanian is separated from mid-Oligocene strata by an unconformity. As reported by Berggren (1972), the base of the Miocene has been drawn by the Committee on Mediterranean Neogene Stratigraphy a short distance above this unconformity at Moulin de Bernachon. The first evolutionary appearance of the *Globigerinoides trilobus* group, which includes several subspecies referred to under different names by different authors, is commonly known as the *Globigerinoides* Datum and is agreed to be closely correlative with the base of the Aquitanian Stage (Bandy 1964, Blow 1969, Berggren 1969, 1972). Other authors have stressed, however, that such correlation cannot be regarded as precise; Scott (1972) has stated that the first evolutionary appearance of *G. trilobus primordius* Blow and Banner precedes the base of the stratotype Aquitanian. In terms of the widely used sequence of Banner and Blow's (1965) planktonic foraminiferal zones, the *Globigerinoides* Datum marks the base of Zone N4 as redefined by Blow (1969).

Using the K-Ar method, Turner (1970) dated volcanic rocks stratigraphically related to the boundary between the Zemorrian and Saucian

TABLE 1

K-AR WHOLE ROCK AGES OF BASALTS AT MAUDE AND AIREYS INLET

Sample No.	K%	Radiogenic ^{40}AR ($\times 10^{-10}$ moles/ gm)	% ^{40}AR (radio- genic)	Age (m.y.)	Locality	
(a) MAUDE BASALT						
69-9	0.887 } 0.886 }	0.887	0.342 0.347	38.3 68.6	21.5 \pm 0.3 21.8 \pm 0.4	Moorabool River, southeast of Lethbridge.
69-10	0.866 } 0.866 }	0.866	0.335	33.8	21.6 \pm 0.4	" "
69-5663	0.917 } 0.913 }	0.915	0.347	53.4	21.2 \pm 0.4	Moorabool River, east of The Pimple hill.
69-5665	0.787 } 0.791 }	0.789	0.295	60.8	20.9 \pm 0.3	Moorabool River, near Lowndes Bridge.
(b) AIREYS INLET BASALT						
69-5667	1.218 } 1.223 }	1.221	0.547 0.581	42.0 61.8	25.0 \pm 0.4 26.5 \pm 0.5	Aireys Inlet, Split Point.
69-5869	1.271 } 1.282 }	1.277	0.607 0.615	35.4 34.2	26.5 \pm 0.6 26.9 \pm 0.6	" "

Constants used: $\lambda = 4.72 \times 10^{-10} \text{ yr}^{-1}$, $\lambda_0 = 0.585 \times 10^{-10} \text{ yr}^{-1}$,
 β

$^{40}\text{K}/\text{K} = 1.19 \times 10^{-2}$ atom percent.

stages in California and concluded that this boundary is about 22.5 m.y. old. Blaeut and Kleinpell (1969) correlated the Zemorrian-Saucesian boundary with the base of Bolli's (1957) *Globorotalia kugleri* Zone, which is equivalent to Zone N4 as originally defined by Banner and Blow 1965 (i.e. its base is slightly higher than the base of Zone N4 as emended by Blow, 1969). Largely on the basis of these conclusions Berggren (1969, 1972) assigned a 22.5 m.y. age to the Oligocene-Miocene boundary, which he equated both with the base of Zone N4 and the *Globigerinoides* Datum. Comparison of the opinions of various authors shows that detailed correlation of the series and stages defined in Europe with the tropical planktonic foraminiferal zones is still rather controversial. Recently Hornaday (1972) has criticized the validity of some such correlations and the hasty application of radiometric dates to some boundaries. Hornaday, following Bandy and Ingle (1970), correlated the top of the Zemorrian Stage with the top rather than the base of the *Globorotalia kugleri* Zone; however, in agreement with Berggren (1969, 1972), both Bandy and Ingle (1970) and Hornaday (1972) regarded the top of the Zemorrian Stage as corresponding closely to the Oligocene-Miocene boundary. Thus, while the base of Zone N4 and the *Globigerinoides* Datum may be slightly older than the base of the stratotype Aquitanian, Berggren's assignment of a 22.5 m.y. age to the Oligocene-Miocene boundary appears to be satisfactory, and the best available estimate.

In southeastern Australia, as elsewhere, precise recognition of the Oligocene-Miocene boundary is difficult. In this region the first appearance of *Globigerinoides trilobus trilobus*, marking the base of zone 7, is a stratigraphically more useful and a later event than the first appearance of the genus. Only rare specimens of *Globigerinoides* (e.g. the form referred to as *G. quadrilobatus primordius* and *G. q. altiapertura* by Wade, 1964) have been recorded from strata recognized as older than zone 7 (including beds as old as zone 5). Thus the *Globigerinoides* Datum is not a reliably recognizable horizon in southeastern Australia; a similar situation exists in New Zealand (Scott 1970, Jenkins 1970).

Carter (1958a, b, etc.) defined the top of zone 5 as coinciding with the disappearance of *Victoriella conoidea* and considered that *Globoquadrina dehiscens* first appears at a slightly higher horizon in zone 6. Other workers, e.g. Wade (1964) and Ludbrook (1971), have noted that in some areas the ranges of the two species overlap; hence Wade considered that *G. dehiscens* appears in zone 5 and Ludbrook that *V. conoidea* ranges upwards

into the lower part of her *Globoquadrina dehiscens dehiscens* Zone. In New Zealand, occurrences of *V. conoidea* also coincide with the lower part of the range of *G. dehiscens* (Hornibrook, 1961). The distribution of the benthonic *V. conoidea* is certainly influenced by variation in facies; however, the planktonic *G. dehiscens* also occurs rather sporadically in strata corresponding to the lower part of its range, being generally absent from strata recognized as representing zone 5 and rare or absent in beds belonging to zone 6. Whether the original definition by Carter of the boundary between zones 5 and 6 is retained or the base of zone 6 redefined as marked by the first appearance of *G. dehiscens*, is not very important for the purposes of the present discussion since in the areas considered here in detail the ranges of *V. conoidea* and *G. dehiscens* are mutually exclusive. In any case, correlation with overseas sequences is complicated by records of first appearances of *G. dehiscens* at apparently different stratigraphic horizons in different regions, as discussed by various authors (among them Jenkins 1970, and McGowran et al., 1971). As also pointed out by McGowran et al., such correlation is further handicapped by the discrepancy between Bolli's (1957) record that *G. trilobus trilobus* first appears at the base of the *Catapsydrax dissimilis* Zone (i.e. at the base of Zone N5) and Blow's (1969) report that this appearance occurs in Zone N6; following McGowran et al. (1971), Blow's opinion is accepted here.

During the last decade the boundary between zones 5 and 6 or a closely corresponding horizon (Glaessner 1959, Wade 1964, Taylor 1966, Ludbrook 1967, 1971, Ludbrook & Lindsay 1969), less commonly the boundary between zones 6 and 7 (Carter 1958 a, b, 1959, 1964, Reed 1965), have been tentatively equated by Australian workers with the Oligocene-Miocene boundary. Recently the Oligocene-Miocene boundary, as corresponding to the base of the intercontinentally applied Zone N4, has been placed slightly below the top of zone 5 by McGowran et al. (1971). This may well be more correct than equating the top of zone 5 with the top of the Oligocene; both estimates are in agreement with Jenkins' (1966) report that *Globoquadrina dehiscens* is present in type lower Aquitanian, while *Globigerinoides trilobus trilobus* appears at a stratigraphically higher level.

If a horizon slightly below the top, or even at the top, of zone 5 is equated with the Oligocene-Miocene boundary, the 21.4 m.y. age of the very early Longfordian Maude Basalt agrees very well with Berggren's (1969, 1972) assignment of a 22.5 m.y. age to the beginning of the Miocene.

STRATIGRAPHIC RELATIONS AND AGE

sections to the northeast the Angahook Member is represented largely by pyroclastic and continental sediments. These overlie the Anglesea Member (comprising both Anglesea Siltstone Member and Addiscot Greywacke Member of Raggatt & Crespin, 1955) of the Demons Bluff Formation.

The Point Addis Limestone Member at Aireys Inlet contains a rather sparse foraminiferal fauna in which planktonic specimens are very rare. The benthonic foraminifera *Victoriella conoidea*, *Sherbornina atkinsoni*, *Calcarina mackayi*, *Astrononion centroplax* and *Amphistegina* sp. are present and *Crespinina kingscotensis* Wade has also been recorded by Raggatt and Crespin

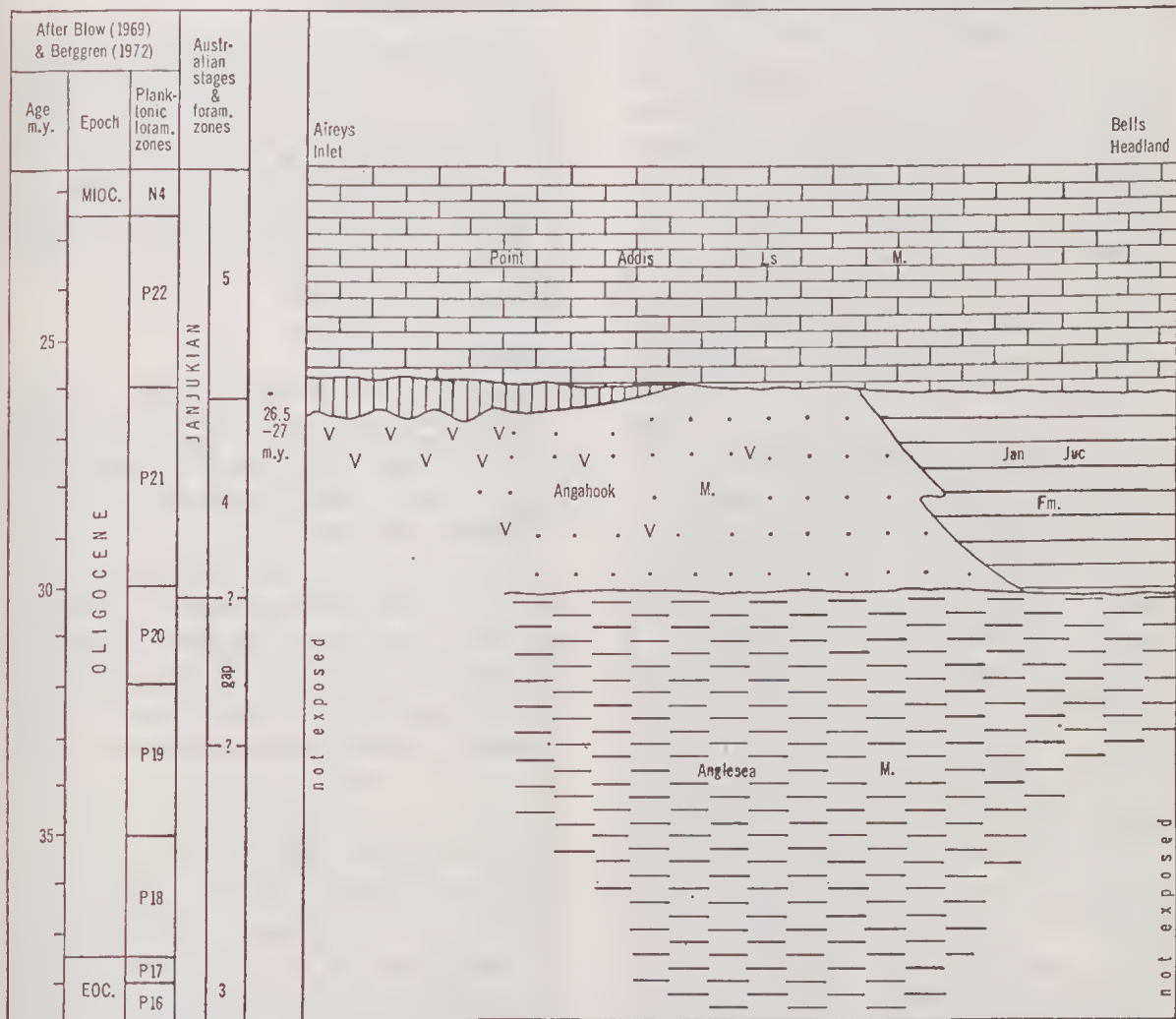


FIG. 4—Stratigraphic relationships at Aireys Inlet and Bells Headland. Between Aireys Inlet and Bells Headland relationships are shown in a generalized way; in most of the coastal exposures the Point Addis Limestone Member has been removed by erosion.

(1955). Paleontologic and stratigraphic considerations, especially comparison with the section at Bells Headland (19 km to the northeast, Figs. 1, 4), make it unlikely that the basal strata of the limestone at Aireys Inlet are as old as zone 4; they are probably slightly younger than the base of zone 5.

Paleontologic dating of the Point Addis Limestone Member provides a reasonably accurate minimum stratigraphic age for the underlying basalt at Aireys Inlet. Estimates of the maximum age of the basalt are based on somewhat equivocal evidence, as discussed in the following paragraph.

In those nearby sections where the Anglesea Member is directly and conformably overlain by the Jan Juc Formation, the Angahook Member has been generally regarded as equivalent in age either to the upper part of the Anglesea Member or to the lower part of the Jan Juc Formation (e.g. Raggatt & Crespin 1955, Singleton 1968). Such a sequence is exposed only at Bells Headland, where the lower part of the Jan Juc Formation, about 15 m thick and overlain conformably by the Point Addis Limestone Member, represents zone 4. *Chiloguembelina cubensis* (Palmer), present in the lowermost part of the Jan Juc Formation, is absent from the uppermost beds of zone 4 as defined by Carter (1958a, b, etc.), who referred to the species as *Gümbelina rugosa*. The upper strata of the underlying Anglesea Member have been somewhat arbitrarily regarded as representing zone 3 or as Upper Eocene in age; very rare planktonic foraminifera have been observed in samples of the member from bores not far from Bells Headland (K. J. Reed, unpublished report 1961, Taylor 1965). It is more probable that in respect to time of deposition these beds span a 'gap' separating zones 3 and 4. The top of zone 3 has been commonly regarded as marked by the disappearance of *Globigerina linaperta* Finlay; the somewhat later disappearance of the closely related *G. angiporoides* Hornibrook may be a more valid criterion since, as observed by Lindsay (1967), McGowran et al. (1971) and other authors, Carter's (1958a) concept of *G. linaperta* apparently included *G. angiporoides*. It appears that extinction of both *G. linaperta* and *G. angiporoides* in Victoria preceded the initiation of deposition of the Jan Juc Formation at Bells Headland. The existence of a 'gap' between zones 3 and 4, based on 'Faunal Units' originally defined from two widely separated areas (the Aire district southwest of the Otway Ranges, and Bells Headland), has been recently implied by Ludbrook and Lindsay (1969). Equating the disappearance of *G. angiporoides* rather than *G.*

linaperta with the top of zone 3 reduces the magnitude of the 'gap', but apparently does not eliminate it entirely; such elimination could be achieved, of course, by extending the definition of zone 4 downwards to include an appropriate interval of strata directly underlying the Jan Juc Formation at Bells Headland.

In short, the available paleontologic and stratigraphic evidence indicates that the basalt at Aireys Inlet is definitely no younger than the lowermost part of zone 5 (late Janjukian). On the basis of considerably less certain evidence the basalt may be regarded as no older than zone 4, but the possibility that it is as old as zone 3 cannot be excluded.

ISOTOPIC DATING

Two whole rock samples of basalt from Split Point (Aireys Inlet) have been dated by the K-Ar method in duplicate (Table 1). The two mean ages of 25.8 m.y. and 26.7 m.y. agree to within experimental error, but as the two measurements on sample 69-5667 are not quite concordant, it is suggested that the older age of 26.7 m.y. may be the more meaningful estimate. These limited data point to a 26.5 to 27 m.y. minimum age of the basalt at Aireys Inlet.

DISCUSSION

In recent years it has been generally agreed by Australian workers that the top of the Eocene in southeastern Australia is best recognized as marked by the disappearance of *Globigerina linaperta* (Wade 1964, Lindsay 1967, Ludbrook & Lindsay 1969, McGowran et al. 1971); this contrasts with Blow's (1969) report that *G. linaperta* disappears within Zone P16 rather than at the top of Zone P17. However, as discussed previously, there is some uncertainty concerning the criteria defining the top of zone 3 and hence as to whether the top of zone 3 should be equated with the top of the Eocene or with a higher Oligocene horizon. According to Blow (1969), the related *G. angiporoides* ranges upwards into the lower part of Zone P19. Zone 4 has been generally regarded as representing an early Oligocene (Wade 1964, Singleton 1968) or a mid-Oligocene (Ludbrook 1967, Ludbrook & Lindsay 1969, McGowran et al. 1971) time interval. The top of zone 4 is not far above the disappearance of *Chiloguembelina cubensis*; both Berggren's (1972) assignment of a 28 m.y. age (i.e. within Zone P21) to the *Chiloguembelina* (extinction) Datum and Blow's (1969) report that this genus ranges even higher, at least up to the top of Zone N3, favour the mid-Oligocene estimates of the

age of zone 4. The top of the range of *C. cubensis* in southeastern Australia appears to agree well with Berggren's *Chiloguembelina* (extinction) Datum, but, as indicated by McGowran et al. (1971), to be lower than the top of the range of '*Chiloguembelina* ex group *cubensis*' reported by Blow.

In contrast to the Maude Basalt, the basalt at Aireys Inlet cannot be firmly dated on the basis of paleontologic and stratigraphic evidence since reliable evidence in respect to its maximum stratigraphic age is lacking, as discussed previously. Thus the K-Ar age of the Aireys Inlet basalt cannot be readily applied in either supporting or contradicting Berggren's (1972) time scale. However, the dating of the basalt provides valuable evidence for local stratigraphic interpretation and correlation. The 26.5 to 27 m.y. age of the basalt at Aireys Inlet, corresponding to mid-Late Oligocene on Berggren's time scale, indicates that the basalt is equivalent in age to the upper part of zone 4. Apparently the unconformity between the basalt and the overlying limestone, though spectacular in expression, represents a brief interval of non-deposition. Although the available paleontologic and stratigraphic evidence has permitted consideration of the Angahook Member as representing a time interval near the Eocene-Oligocene boundary (Ludbrook 1967, Singleton 1968), the K-Ar age of the Aireys Inlet basalt suggests that the Angahook Member is Middle to Late Oligocene (i.e. Late Oligocene on Berggren's time scale), equivalent in age to zone 4 rather than zone 3 and to the lower part of the Jan Juc Formation rather than to the upper part of the Anglesea Member of the Demons Bluff Formation.

In addition, the radiometric age of the basalt at Aireys Inlet indicates that zone 5 is no older than 26.5 to 27 m.y. As discussed previously, isotopic dating of the Maude Basalt suggests that the zone (and the Janjukian Stage) is no younger than 21.4 m.y. Thus zone 5 appears to represent a time interval of not more than 5 to 5.5 m.y.

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APPENDIX

SAMPLE DESCRIPTIONS OF THE BASALTS USED IN K-Ar DATING

69-9, 69-10 Moorabool River, 2 km south-east of Lethbridge. Porphyritic olivine-augite basalts, containing phenocrysts of olivine (cracked and slightly serpentinized), clinopyroxene and rare plagioclase ($\sim \text{An}_{50}$). Groundmass consists of abundant prismatic plagioclase laths with a crude flow texture, intergranular clinopyroxene and minor olivine. There is some interstitial chlorite and parts of the groundmass are peppered with opaque material.

69-5663 Moorabool River, 1.5 km NW. of 69-5665. Porphyritic olivine basalt, consisting of partly serpentinized olivine phenocrysts in a fairly coarse matrix of plagioclase, colourless clinopyroxene, olivine and opaque granules. Minor sphene and chlorite are present.

69-5665 Lowndes Bridge, Moorabool River. Porphyritic olivine basalt, similar to 69-5663, but with abundant pink titan-augite in the groundmass. Virtually no chlorite present.

69-5667, 69-5869 Split Point, Aireys Inlet. Porphyritic olivine basalt, with olivine almost entirely pseudomorphed by serpentine mineral. The euhedral fresh plagioclase and clinopyroxene phenocrysts are set in a holocrystalline intergranular groundmass of plagioclase, opaque mineral and clinopyroxene. Irregular chloritic patches are present in 69-5667.

FOSSIL PENGUIN BONES FROM MACQUARIE ISLAND, SOUTHERN OCEAN

By A. R. McEVEY¹ AND W. J. M. VESTJENS²

WITH APPENDIX BY EDMUND D. GILL³

ABSTRACT: Fossil bones of *Eudyptes chrysolophus schlegeli* Finsch, c. 6000 years old, and of *Aptenodytes patagonica* Miller, c. 4000 years old, from Macquarie Island are compared with recent bones of these species to reveal no significant difference. An account is given of the fossil beds at Finch Creek and of previously unrecorded beds at Bauer Bay. Evidence of an early and hitherto unrecorded colony of *Aptenodytes patagonica* at Bauer Bay is thus established. Comment on the terminology of the penguin skull and humerus is included. An appendix on the geology is provided by E. D. Gill.

INTRODUCTION

Macquarie Island (lat. 54° 30' S., long. 159° 00' E. map Fig. 1) may be conveniently described as 'a mountain range rising abruptly in cliffs directly from the sea, or from narrow low-lying bcaehes' (Mawson 1943). Finch Creek flows southeast into Sandy Bay on the east coast some five to six miles south of North Head. Strata containing fossil penguin bones occur in the south bank, the original find being made at a point just west of the junction with the creek's lowest tributary (Fig. 2). They are now known to extend both west and east of this point.

The first published reference to the bones from Finch Creek is by L. R. Blake, whose extensive geological and topographical notes formed the basis of Sir Douglas Mawson's Report (1943) on Macquarie Island in the Scientific Reports of the Australasian Antarctic Expedition, 1911-14. His note, with sketches, remarks 'bird bones . . . sparsely distributed, . . . in all probability those of a species of penguin, . . . too fragmentary and decomposed to allow of specific determination'. It is not known whether Blake, or anyone else during that period, collected specimens.

Mawson's footnote ('too fragmentary and decomposed to allow of specific determination') may be read as evidence that Blake had collected fragments, that Mawson had seen them ('he handed over to me all his specimens and photographs'), and had considered them not worth

preserving. Alternatively it is possible that Blake, finding only fragments and making no collection, mentioned their condition to Mawson. After a lapse of nearly 40 years a collection of bones was made in 1949 by Dr. A. M. Gwynn and deposited in the National Museum of Victoria.

In December 1957 one of us (McEvey) visited Macquarie Island to study the occurrence, found an extension of the strata, made a further collection, and initiated research on the specimens. During 1962 the other author (Vestjens) spent 12 months on Macquarie Island as biologist. He undertook further study of the Finch Creek occurrence, made the largest collection, found an extension of the strata to the east and discovered previously unknown fossiliferous strata at Bauer Bay. The aims of the present paper are to summarize the stratigraphy, list the fossils and make osteological comments.

PENGUIN OSTEOLOGY

It would appear that no detailed description of the skeleton of either the Royal Penguin (*Eudyptes chrysolophus schlegeli* Finsch) or the King Penguin (*Aptenodytes patagonica* Miller) has been written.

A useful bibliography to the early taxonomic history of the penguins is provided by Coues (1872). Subsequent valuable papers by early workers on the osteology of the group are by Watson (1883), Menzbier (1887) and Pycraft (1898).

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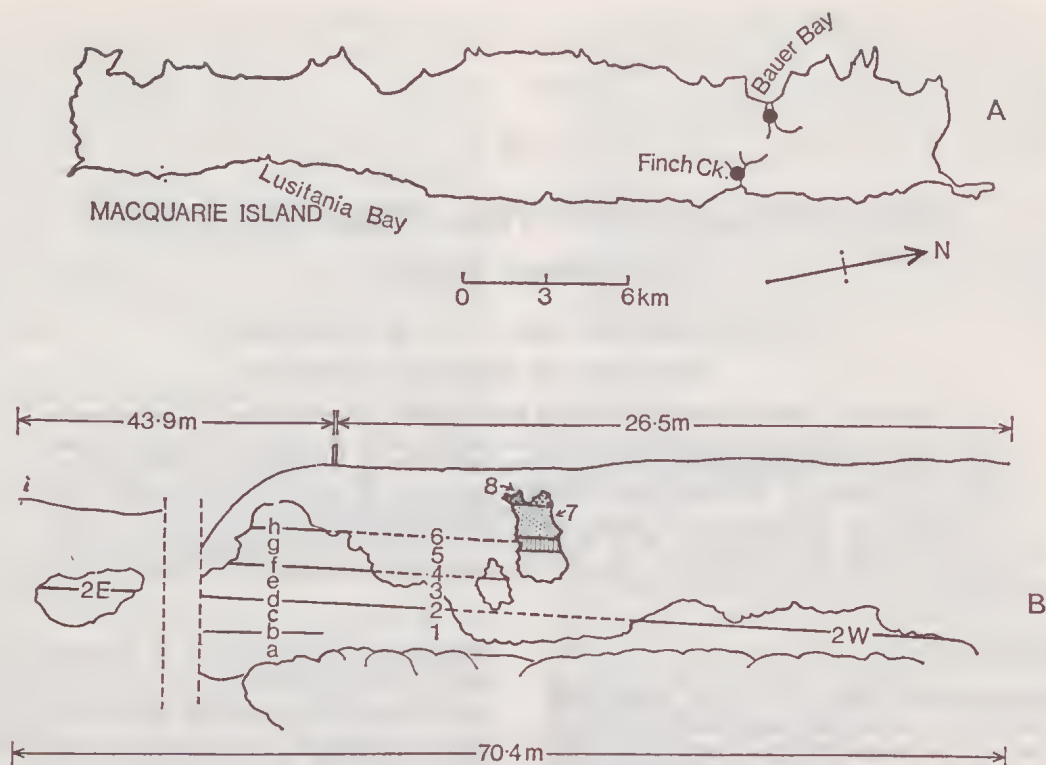


FIG. 1—(A) Macquarie Island showing positions of Finch Creek and Bauer Bay. (B) Finch Creek strata. Lettered as by Blake, numbers by present authors. Included are extensions 2 E and 2 W, and Vestjens' exposed upper beds. (Drawing: F. Knight).

Watson (1883) remarks, 'In the works of none of the authors above named, however [Blumenbach, Brandt, Wagner, Eyton and Barkow], can I find any approach to a complete comparative description of the various species of Penguin, and this deficiency I now endeavour to make good, so far as material at my disposal will permit'. His ensuing account, excellent as it is, discusses eight species including *chrysolophus* from Kerguelen Island and is necessarily somewhat general. A rather more precise treatment of the penguin skull, for example, is provided by Pycraft (1898).

However, full descriptions of skeletons of single species are perhaps not the most pressing need in cases such as this where the morphology of the family, by comparison with that of other families of birds, is so little varied.

In the absence of a full osteological description of the living sub-species *E. c. schlegeli*, for use as a basis for comparison with fossil specimens, the notes of Watson (1883), Pycraft (1898) and Marples (1952) are used as fundamental references and the opportunity is taken to comment upon one or two points of terminology.

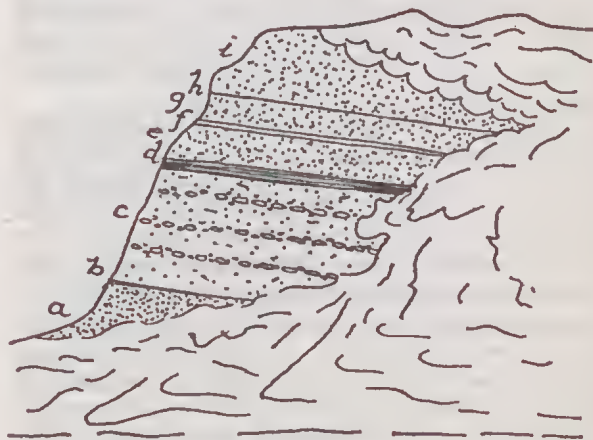


FIG. 2—Strata at Finch Creek. The legend in Mawson reads: 'Fluvio-glacial deposits in Finch Creek. (a) Gravel and Sand; (b) Peaty Mud—1 inch; (c) Coarse Sand Gravel with occasional bird bones—6 ft. 6 inches; (d) Peaty Mud—9 inches; (e) Gravel and Sand—18 inches; (f) Peaty Mud—3 inches; (g) Gravel and Sand—18 inches; (h) Peaty Mud—1 inch; (i) Sand and Gravel—3 feet plus.' (Drawing: L. Arnold, after Blake in Mawson, 1943, Fig. 40 p. 83).

Beddard (1898) lists the family Spheniscidae (Penguins) as being schizognathous in its palatal arrangement and *E. c. schlegeli* typifies this, the vomer being anteriorly pointed, and posteriorly, clasping the basisphenoid between the palatines. The palatines, together with the pterygoids, are not, however, separated by the vomer, but themselves articulate with the basisphenoid. Garrod (1873) lists Impennes (Sphenisciformes) as having holorhinal nasal bones. *E. c. schlegeli* exemplifies this condition. The nasal opening ends posteriorly well anterior to the nasal-frontal hinge and does not separate the hinge-line of the lateral nasal bars from that of the medial dorsal bar (Bock & McEvey 1969, p. 205). The skull is prokinetic (cf. Bock 1964). The posterior margin of the nasal opening is incidentally rounded.

Bock (1960) pointed out that a secondary articulation of the mandible is present in *Aptenodytes* and remarks that 'it is absent (?) in others such as *Spheniscus*'.

Examination of skulls that have not been prepared with particular attention to this region can be very misleading because capping pads on articular surfaces are frequently removed and quadrates and mandibles are often found to have dried in positions which might or might not be natural and therefore provide uncertain evidence as to the amount of space normally found between the medial process of the mandible and the lateral/medial process of the basitemporal plate, in the species concerned. Thus in specimens of the same species one can find dried skulls showing gradations from obvious evidence of secondary articulation by the actual abutting of the processes mentioned with surfaces clearly shaped for

articulation, to doubtful evidence where although the surfaces correspond in shape for possible articulation, the gap between them is so wide (possibly caused by the quadrate drying in a twisted position) that they can be brought closer together only by force disturbing the natural position of the bones. Soaking the skull to produce freer movement is unsatisfactory because even then one cannot be certain that the quadrate is in a truly normal position, and the complex shape and action of this bone are such that a very slight movement of it has a magnified effect upon the position of the medial process of the mandible in relation to the basisphenoidal plate. Even when the specimen shows actual contact between the basitemporal process and the mandible one cannot be certain that the quadrate is in the exact position it would hold in life. From the limited number of recent skulls examined (i.e. examples carrying quadrates and mandibles intact) the authors, pending further examination by dissection, tentatively classify the subspecies *E. c. schlegeli* as exhibiting secondary articulation, but suggest that it is not as well developed as in the genus *Aptenodytes*.

For general details of the skull the notes by Pycraft (1898) are particularly relevant. It may be noted that the 'temporal crest' of Watson appears to be the 'squamoso-parietal wing' or 'plate' of Pycraft. The edge of this forms a continuation of the supraoccipital (lambdoidal) ridge. In the basioccipital region Pycraft's 'mammillary process(es)' (p. 961) is the medial process

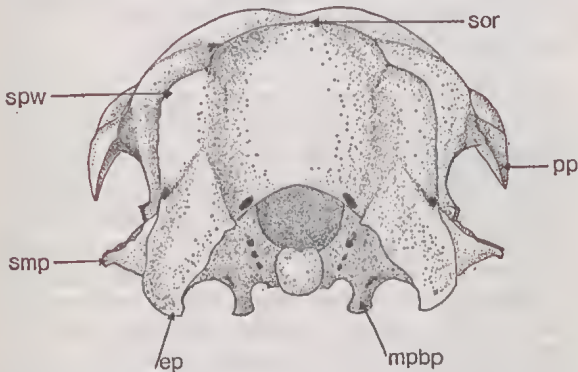


FIG. 3—Diagrammatic sketch of skull of *E. c. schlegeli*, posterior aspect. sor = supra-occipital (lambdoidal) ridge, spw = squamoso-parietal wing, pp = postorbital process, smp = supra-meatic process, ep = exoccipital process, mpbp = medial process of basitemporal plate. (Drawing: L. Arnold.)

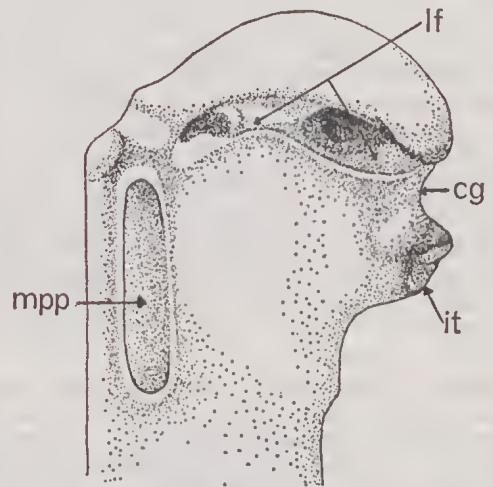


FIG. 4—Diagrammatic sketch of head of humerus of *E. c. schlegeli*, ventral aspect. lf = ligamental furrow, cg = capital groove, it = internal tuberosity, mpp = insertion of *M. pectoralis primus* (= major). (Drawing: L. Arnold.)

of the basitemporal plate. The terminology applied to bones in this region has been confusing in the past and Fig. 3 illustrates some of the names used in the present paper. (See also Bock 1960, pp. 38 and 40.)

Concerning the humerus (see Fig. 4) it is of interest to note the terminology used by Watson (1883) and Marples (1952). The crescentic form of the caput or head of the humerus mentioned by Watson is seen when the head is viewed end-on. The 'horizontal groove which affords attachment to the capsular ligament of the shoulder joint' of Watson (p. 29) and the 'capsular groove' of Marples (p. 17 and diagram p. 9) are the 'ligamental furrow' of Howard (1929) and, as a more recent example, Bock and McEvey (1969).

The 'horizontal groove' of Watson (p. 29) and 'a slight groove' of Marples (under 'Shape of Capsular Groove', p. 17) both appear to be the 'capital groove' of Howard, Bock and McEvey and others, and 'the incisura capitis' of Newton (1893-6, p. 439).

In many birds, e.g. Turnix, the ligamental furrow and capital groove are distinctly separated by a ridge. In *Eudyptes c. schlegeli* they are virtually continuous though running at different angles and only the narrowing of the ligamental furrow separates them. In *Aptenodytes*, as Marples points out, there is even less separation between the two regions.

Also in the wing bones it may be noted that the 'ulna carpal' bone of Watson (1883) is the 'pisoulnare' of Bellairs and Jenkin (1960). In the carpometaarpus the interpretation of the metacarpals varies, that used by Watson and Marples differing from that given by Bellairs and Jenkin in the numbering of metacarpals 1, 2 and 3. The numbering as given by Marples is accepted here.

The present study centres on fossil bones of *E. c. schlegeli* known to be 6000+ years old. The biological problem is to determine whether evolutionary change in the species has occurred during this period. The bones provide an opportunity for osteological examination and analysis of measurements, on the basis of comparison of fossil with recent bones. The study is carried further with an examination of fossil bones of *Aptenodytes patagonica*.

Bones of both species were found on Macquarie Island at both collecting sites, Finch Creek and Bauer Bay (Fig. 1A). Since the majority of bones from Finch Creek were of *E. c. schlegeli* (see Table 1), this species is discussed in connection with this site. Similarly, *Aptenodytes patagonica* is discussed in connection with the Bauer Bay site, where its bones were found more abundantly than those of *E. c. schlegeli* (Table 3).

FINCH CREEK SITE

The fossil beds are exposed in the south bank near its junction with the lowest tributary and east to the beach. The bank is overgrown with Macquarie Island Cabbage *Stilbocarpa polaris*, Tussock Grass *Poa foliosa* and Fern (Pl. 8, figs. 1-4). The acidic ground water has decomposed bones. A path several feet wide made by Royal Penguins (Pl. 8, fig. 1) along the creek bank at about mid-height provides a platform from which the most productive stratum can be reached. The stratigraphic succession is shown in Fig. 1B. Mawson (1943), Ivanac (1948) and Law and Burstall (1956) comment on the geology.

A sample of the bones of the Royal Penguin from strata (d) and 2 W from the McEvey and Vestjens Collections was assayed by Professor Kigoshi (GaK- 643) as $6,100 \pm 120$ y. B.P.

FINCH CREEK COLLECTIONS

The stratigraphic occurrence of these Collections is listed in Table 2.

Gwynn Collection: Bones of *E. c. schlegeli* (Table 1) were taken from Blake's section in 1949. They comprise leg bones, vertebrae, carpo-metacarpal, coracoids, humeri, pelvic girdle parts and cranial parts.

McEvey and Whitten Collection: This was made on 13th and 17-18th December 1957. The most significant event was finding an extension of Blake's fossiliferous stratum (d) some 70 m upstream (see Pl. 8, fig. 2). Most of the fossils collected were obtained from Blake's stratum (d) and its western extension. An unsuccessful search for 300-400 m upstream was limited to exposed patches and sites selected at random. Many specimens crumbled at touch. A few bones of species other than penguins were collected but are excluded from the present study.

Vestjens Collection: Several visits were made during 1962 and Messrs. Pederson and Vestjens searched for extensions of the known fossil area. The creek was examined on both sides for approximately 800 m west of the tributary by digging at least every 9 m. The top of the coastal cliff, north of the creek, was searched along approximately 91 m and places approximating in height to the known fossil strata were extensively checked. The banks of the tributary south of Blake's section, and the south bank of Finch Creek east of Blake's section were also examined. Searching was difficult because of the thick plant cover and the top layer of peat. A layer was found in the south bank of the Creek east of the tributary, approximately 43 m from the stake inserted by McEvey (Pl. 8, fig. 4) above the

Blake's Section			Fossils	Vestjens' Section		Fossils
i. Sand & gravel	91	cm plus	None	119	cm	Some bones
h. Peaty mud	2.5		None	28		
g. Gravel & sand	48		None	61		
f. Peaty mud	7.5		None	52		None
e. Gravel & sand	48		Some bones	85		Some bones
d. Peaty mud	23		Some bones	20 ±		Numerous bones
c. Coarse sand gravel	198		Some bones	Checked for 152	cm	Some bones
b. Peaty mud	2.5		—	—		—
a. Gravel & sand	—		—	—		—

centre of Blake's section. By this discovery the known fossil area was increased to an overall length of c. 70 m. Collecting was done at Blake's section but the material was saturated and difficult to dig out. Blake's stratum (d) contained in addition, seeds of *Stilbocarpa polaris* at a depth of c. 20 cm. The main collecting was done in stratum 2 W. From McEvey's stake this layer extended for about 26.5 m and averaged about 20 cm in depth with a maximum of 24 cm. At the end of the extension the layer dwindled to 5 cm in depth and no fossils were found in it. Fossils in this layer were well preserved and Pl. 8, fig. 3 shows them *in situ*.

A new (Vestjens') section, on the McEvey extension of Blake's section was exposed c. 8 m west of the stake. It is shown by white squares at right of Pl. 8, fig. 4 and is also shown in Fig. 1B. A comparison of Blake's section (Fig. 2) and Vestjens' section is shown above.

E.c. schlegeli

OSTEOLOGICAL EXAMINATION (Table 5): The fossil bones (Table 1) and recent bones examined and compared were the humerus, radius, ulna, pisoulnare, carpometacarpus, phalanges of manus, coracoid, clavicle, scapula, femur, tibio-tarsus, tarso-metatarsus, phalanges of pes, ilia-ischia, synsacrum, sternum and skull.

Particular attention was given to muscle scars, conformation of condyles, processes, and fossae, and to any other features in which change, where it has occurred, would be readily discernible. Careful examination of all aspects of the bones, however, reveals a marked individual variation in many characters in both fossil and recent forms. Within this variation in size and conformation one can easily find fossil and recent bones matching so closely that any differences found are likely to be merely individual ones.

This, broadly, is the conclusion reached by osteological examination. The only exceptions occurred in connexion with the humerus and coracoid. In the humerus the groove of insertion of *M. pectoralis primus* tends, at its distal end, to be wider and shallower in the fossil than in the recent. Though very small in extent this difference is distinctly perceptible. The series of measurements shows that

the left fossil humerus averages 3.5 mm against 3.1 in the recent bones. The right fossil humerus averages 3.9 mm against 3.25 in recent bones. This incidentally displays an interesting, though (from the evolutionary viewpoint) not necessarily significant larger insertion on the right than on the left in both fossil and recent forms.

In the coracoid the inclination of the coracohumeral surface (i.e. the angle of turn from the longitudinal axis of the bone) gives the appearance of a slightly greater inclination in recent than in fossil bones. A technique devised for measuring this showed only 0.4° difference of inclination in the left coracoid and only 0.5° difference in the right. The variation of surface features affecting this measurement render it difficult to obtain stable figures.

STATISTICAL ANALYSIS: Tables 5 and 6 show (i) extreme and mean values of several measurements of each bone and (ii) variances for two selected measurements of each bone.

On the level of simple comparison of means (fossil v. recent) for all measurements, it will be found that no clear pattern emerges to distinguish fossil from recent bones, though one can find a very slight tendency for the shafts of bones to be narrower in recent than in fossil forms.

Examination of the variances as calculated for two selected measurements of each bone, though a significant difference for both measurements of the humerus may be noted, reveals in general no significant difference between fossil and recent bones. The variances mentioned in connexion with the humerus are not considered to alter the overall conclusion. There is a tendency for the Finch Creek sample to show greater variance than does the recent sample, but this does not occur at a significant level.

The statistical analysis is therefore in accord with the osteological examination, supporting the conclusion that no significant change in the osteology of the species has occurred.

It should be noted that the recent bones, though all collected at the north end of the island, could, on the basis of recorded knowledge of penguin movement, include specimens from any colony round the island. It seems reasonable to assume that birds providing the specimen bones from the Finch Creek population of earlier times could, for the same reasons, represent colonies other than the Finch Creek one. On these grounds the comparison between the two collections is considered justifiable.

BAUER BAY SITE

The only present day colony of the King Penguin (*Aptenodytes patagonica*) at Macquarie Island is on the southeast coast at Lusitania Bay.

In October 1962 Vestjens, searching for areas similar to the coastal flat at Lusitania Bay, found the first fossil humerus of a King Penguin at Bauer Bay (Fig. 1A). In November and December fossils were collected from seven places (Fig. 5), which suggested that a colony had been situated between the two unnamed creeks at the northern end of the Bay.

A sample of 330 g of small parts of the fossil bones was assayed by Professor Kigoshi (GaK 644) as $3,980 \pm 140$ y. B.P.

THE KING PENGUIN AT MACQUARIE ISLAND

The known history of the King Penguin at Macquarie Island since its discovery is outlined by Mawson (1943). 'There now exists only one rookery, located at Lusitania Bay', he states. 'They have been exterminated from other areas as a result of uncontrolled exploitation for blubber oil'.

The following extracts from Mawson's account (p. 39 et seq.) trace the stages of this extermination.

When the Island was discovered there were in existence at least two very large breeding communities. That at Lusitania Bay was vastly greater than it is today, and at the North-End Isthmus there was a second, probably still greater, congregation of birds . . .

A. Hamilton, in his account of life on the Island, states that a large King Penguin rookery was reported at the North End by Bennett in 1815. In 1820 Bellingshausen, who called at the North End but did not visit Lusitania Bay, describes landing amongst a dense population of King Penguins.

A. Hamilton, in 1894, and H. Hamilton, in 1911, both found masses of King Penguin bones buried under drifted sand on the Isthmus, supplying evidence consistent with the former existence of this King Penguin rookery. Probably within thirty years of Bellingshausen's visit, this entire community had been wiped out, for by the year 1820 fur seals were so scarce that the energies of the sealers were mainly devoted to the production of blubber-oil. Production of this oil, apart from that proceeding from the whale fisheries, was firstly obtained by the slaughter of sea-elephants, and secondly from the wholesale destruction of penguins . . .

At the time of Professor Scott's visit (1880) the rookery at Lusitania Bay was still on a grand scale. It was even so when A. Hamilton (1894) reached the Island. He stated that when anchored in 15 fathoms off Lusitania Bay, thousands of King Penguins played around the ship. On shore nearly the whole of the Lusitania Beach . . . and from the

crown of the beach to the hills, was occupied with Kings packed so closely that there remained unoccupied only a space of about 1½ feet in width surrounding each bird. The total area of the rookery he estimated at 30 to 40 acres . . .

In 1895, when Bickerton spent a short time with the sealers, there was still a very large penguin population at Lusitania Bay, for he wrote of them: 'When we reached the rookery the penguins were there in countless numbers' . . .

It must have been soon after Bickerton's visit that a great assault was made upon them, leaving only a remnant which has been and still is in danger of complete extinction. Owing to the fact that only one egg is laid each year, this bird is very slow to increase its numbers . . .

At the time of our occupation (1911) the sealers had ceased to operate at Lusitania Bay . . . however . . . sealers continued to visit Lusitania Bay annually to collect and store for food large quantities of the eggs of the King Penguin . . .

The rookery at Lusitania Bay is the only community of these birds existing within the great sweep of Southern Ocean between Heard Island and Tierra del Fuego. It now comprises about 5000 birds, a mere shadow of its former population.

(Carriek (1957) remarks: 'A large colony of King Penguins at the Isthmus, the narrow neck of land near the north end . . . was wiped out [by sealers] but the other colony at Lusitania Bay near the south end still flourishes.'

Location of the fossils at Bauer Bay suggests that about 4,000 years ago, colonies of King Penguins at Macquarie were either more numerous than, or differently situated from those mentioned in the recorded history of this species.

DESCRIPTION OF FOSSIL SITES

The area within which the fossils were found was 186 m from north to south, 148 m from east to west, and 210 m from the Bauer Bay beach (Fig. 5). No digging could be done on the western part and it is possible that the fossiliferous strata extend in this direction but have been covered by a past landslide. A layer of large pebbles c. 25.5-33 cm in diameter, which represents a top stratum with fossils, extends down at the western end and disappears under the present bedding.

Five of the fossil sites were found along the present 'First Northern Creek' and one at the 'Second Northern Creek' (Fig. 5). They were on creek-bends where water had denuded sand from the outer curves, exposing bones. The largest site was found in a curve of an old creek bed (Fig. 5, D). Here the section exposed (Fig. 6) was half-moon in shape and 35 m long.

Taylor (1955, pp. 86-7) states of this area, 'The sub-soil is sea-worn sand (fragmented

basalt) formed under water. After the ice age, as the raised beach was formed, this sand was elevated above the sea and some of it was blown a little way inland'.

Of soil samples Mr. K. G. Bowen (*in litt.* Jan. 24, 1966) remarks, 'They are all extremely poorly sorted with a very wide distribution suggestive of a fluviatile deposition . . . Blake considers them to be fluvio-glacial in origin. Whether the gravel deposits at Bauer Bay are also fluvio-glacial or not, I am not sure'. For grain size analysis, see Table 7.

Two Royal Penguin colonies at present inhabit the top of the fossil area. Plant associations around the creeks consist mainly of *Pleuro-*

phyllum hookeri, *Stilbocarpa polaris* sub-association, and, on the sand dunes, *Poa foliosa*.

FOSSILS AND FOSSIL LAYERS

The fossils, soft saturated and readily crumbling, were situated indiscriminately, but generally represented complete skeletons rather than random bones, except in the lower layers. This, however, could mean that only the stronger bones of the lower layers, e.g. humerus and femur, were preserved.

The section of site D (Fig. 6) can probably be taken as a section representing the other sites, too, there being only very slight differences between them. It seems that the layers have been

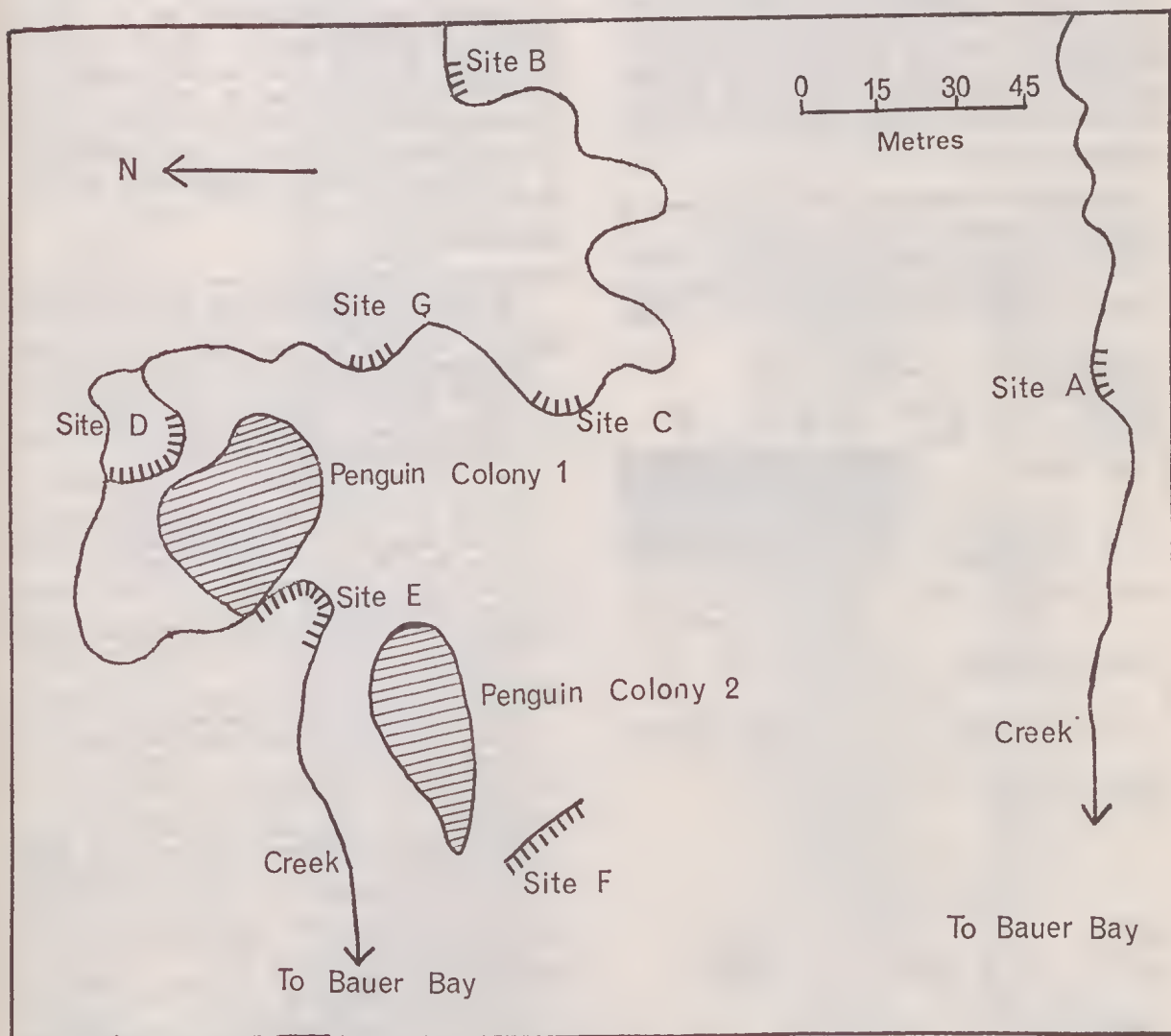


FIG. 5—Fossil sites (A-G) at Bauer Bay, and sites (1 and 2) of present colonies of *E. c. schlegeli*. (Drawing: L. Arnold.)

pushed up under the present colonies (1 and 2, Fig. 5) of Royal Penguins. The pebble layer starts on a lower level under colony 2 (sites F and E) and rises to the level of the inland colony (1) where it has been cut by section site D, and later it appears at site B where it slopes down under the present creek level.

Aptenodytes patagonica

OSTEOLOGICAL EXAMINATION (Table 5): The fossil sample for this species is so limited (Table 3) in material for examination that one can merely group the fossils from Bauer Bay and Finch Creek together, for comparison with recent bones and say that in the humerus, radius, ulna, carpo-metacarpus, phalanx of manus, coracoid, scapula, femur, tibio-tarsus, tarso-metatarsus, phalanx of pes and ilia-ischia, there are no apparent differences to be found in the fossil bones compared with recent bones that cannot be regarded as examples of individual variation.

STATISTICAL ANALYSIS (Table 6): The statistical analysis, based on extremely meagre data, shows no significant difference between fossil and recent bones.

CONCLUSION

Osteological examination and measurement of a limited amount of fossil material of *E. c. schlegeli* show no consistent evidence of evolutionary change. This negative result implies a fair degree of morphological stability in this species

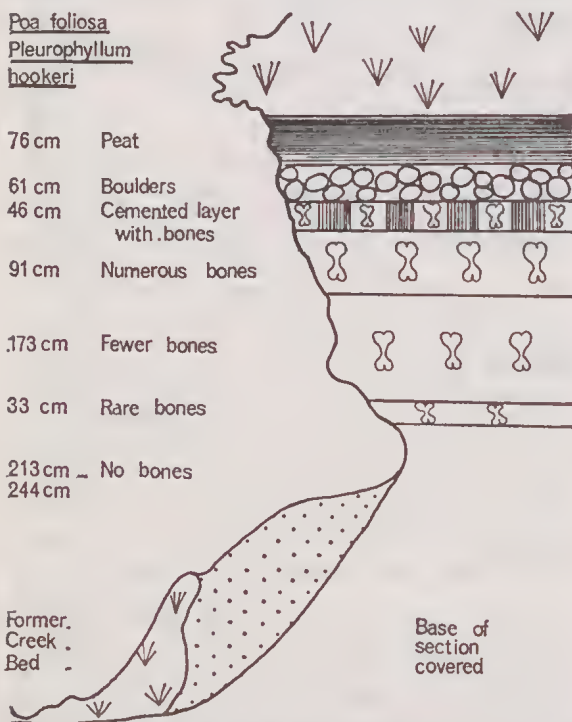


FIG. 6—Section of fossil site D and Bauer Bay. (Drawing: L. Arnold.)

as represented on Macquarie Island during the last 6,000 years.

Results of a similar examination of a much smaller sample of fossil bones of *Aptenodytes patagonica* suggest that a parallel stability has been maintained in this species for the past 4,000 years. The fossil remains of both species provide evidence of former colonies that do not now exist, in certain localities.

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TABLE 1

E. c. schlegeli: FOSSIL BONES COLLECTED AND EXAMINED

	Number in N.M.V. Collection Register
FINCH CREEK	
41 Humerus	B6226, B6230, B9644, B9657
14 Radius	B9648, B9661
19 Ulna	B6225, B9649, B9662
11 Pisoulnare	B10582
17 Carpometacarpus	B6225, B9650, B9663
15 Phalanx of manus	B9675, B10583-5
49 Coracoid	B6226, B9653, B9666
18 Clavicle	B6225, B9652, B9665
11 Scapula	B6225, B9670
61 Femur	B6224, B6230, B9645, B9658
47 Tibio-tarsus	B6224, B9646, B9659
17 Tarso-metatarsus	B6226, B9647, B9660
75 Phalanx of pes	B6225, B9671-2
28 Ilium-ischium	B6225, B9656, B9669
24 Synsacrum	B6227, B9655, B9668
16 Sternum	B9651, B9664
59 Skull (including 39 bill pieces)	B6226, B6236, B9654, B9667, B9676, B9677
53 Vertebra	B6225, B9673-4
2 Pygostyle	B10586
13 Quadrate	B9672
2 Unidentified Bones (fragments)	B6224
BAUER BAY	
10 Humerus	B10574
1 Radius	B10581
4 Coracoid	B10577
4 Femur	B10579
7 Tibio-tarsus	B10578
3 Ilium-ischium	B10576
3 Synsacrum	B10580
2 Vertebra	B10575
COLLECTIONS	
Gwynn:	
Finch Creek 1949	B6224-7, B6230, B6236
McEvey & Whitten:	
Finch Creek 1957	B9644-56, B9675-6
McEvey/Whitten & Vestjens:	(Collections of vertebrae combined) B9673-4
Vestjens:	
Finch Creek 1962	B9657-72, B9677, B10582-6
Bauer Bay 1962	B10574-81

TABLE 2

E. c. shlegeli: STRATIGRAPHIC OCCURRENCE AT FINCH CREEK

GWYNN COLLECTION: These bones were collected from Blake's strata.

McEVEY & WHITTEN COLLECTION: The bones in this collection were collected chiefly from Blake's stratum (d) and the western extension of this, i.e. stratum 2 W, as exposed by McEvey.

VESTJENS' COLLECTION:

Stratum	No. of Bones	N.M.V. Collec- tion Register
Blake's (d)	1 Radius	B9661
	1 Phalanx of pes	B9672
Blake's (f)	1 Humerus	B9657
	1 Coracoid	B9666
	1 Ilium-ischium	B9669
	1 Synsacrum	B9668
	2 Cranium	B9667
2 W	15 Humerus	B9657
	10 Radius	B9661 (plus one in Vestjens Coll.) B9662
	10 Ulna	
	3 Carpo-metacarpus carpus	B9663
	11 Phalanx of manus	B10583-5
	11 Pisoulnare	B10582
	19 Coracoid	B9666
	8 Clavicle	B9665
	12 Scapula	B9670
	28 Femur	B9658
	12 Tibio-tarsus	B9659
	11 Tarso-metatarsus	B9660
	62 Phalanx of pes (excluding ungual phalanx)	B9671
	11 Ungual phalanx	B9671
	12 Ilium-ischium	B9669
	14 Synsacrum	B9668
	2 Pygostyle	B10586
	8 Sternum	B9664
	8 Cranium	B9667
25	Cranial parts (maxill.-pre- maxill.-artic.- angular-splenic)	B9677
13	Quadrate	B9672
	Vertebra (numerous)	

(Continued next page)

TABLE 2 (cont.)

VESTJENS' COLLECTION:		
Stratum	No. of Bones	N.M.V. Collection Register
4 (as exposed by Vestjens)	1 Humerus 1 Ulna 1 Coracoid 3 Femur 4 Tibio-tarsus 1 Ilium-ischium 4 Sternum 1 Cranium 5 Cranial parts (maxill.-pre-maxill.-artic.-angular-splenal)	B9657 B9662 B9666 B9658 B9659 B9669 B9664 B9667 B9677
Unidentified (immediately above 2 W as exposed by Vestjens)	2 Humerus 1 Femur 3 Tibio-tarsus 2 Ilium-ischium 1 Cranium	B9657 B9658 B9659 B9669 B9667
6 (as exposed by Vestjens)	4 Humerus 1 Carpo-metacarpus 2 Coracoid 1 Femur 1 Ilium-ischium 2 Synsacrum	B9657 B9663 B9666 B9658 B9669 B9668
7 (as exposed by Vestjens)	Bone fragments	

TABLE 3

Aptenodytes patagonica: FOSSIL BONES COLLECTED AND EXAMINED

		Number in N.M.V. Collection Register
FINCH CREEK		
3 Humerus		B6229, B10595
1 Radius		B10596
1 Ulna		B10587
2 Carpo-metacarpus		B10588, B10597
1 Phalanx of manus		B10614
2 Coracoid		B6229, B10589
1 Scapula		B10590
1 Femur		B10598
3 Tibio-tarsus		B6229, B10591
2 Tarso-metatarsus		B10592, B10599
1 Ilium-ischium		B10593
1 Sternum		B6229
5 Vertebra		B10594
BAUER BAY		
14 Humerus		B10600
8 Radius & ulna		B10601
3 Carpo-metacarpus		B10602
2 Phalanx of manus		B10603
15 Coracoid		B10604

TABLE 3 (cont.)

		Number in N.M.V. Collection Register
1 Clavicle		B10605
2 Scapula		B10606
17 Femur		B10607
c.57 Tibio-tarsus (chiefly fragments)		B10608
12 Tarso-metatarsus		B10609
12 Phalanx of pes		B10610
1 Ilium		B10611
2 Synsacrum		B10612
3 Sternum		B10613
4 Vertebra		B10615

COLLECTIONS

<i>Gwynn</i> :	
Finch Creek 1949	B6229
<i>McEvey & Whitten</i> :	
Finch Creek 1957	B10587-94
<i>Vestjens</i> :	
Finch Creek 1962	B10595-99, B10614
Bauer Bay 1962	B10600-13, B10615

TABLE 4

KEY TO MEASUREMENTS OF VARIOUS BONES,
SEE TABLES 5 & 6

HUMERUS: A Extreme length, B Internal transverse diameter of tricipital fossa, C Minimum width of shaft between the preaxial angle and the head of the humerus, D Width of the shaft at the preaxial angle, E Minimum width of shaft between the preaxial angle and the distal end of the humerus, F Distance from the outer surface of the radial condyle to the border of the dorsal lip of the dorsal sesamoid groove, G Distance from the outer surface of the radial condyle to the border of the ventral lip of the dorsal sesamoid groove, H Distance from the outer surface of the radial condyle to the border of the ventral lip of the ventral sesamoid groove.

RADIUS: A Extreme length, B Maximum preaxial-postaxial width, C Preaxial-postaxial width at the midpoint of the radial shaft, D Transverse depth of the radial shaft at its midpoint.

ULNA: A Extreme length, B Maximum preaxial-postaxial width (i.e. at proximal end), C Preaxial-postaxial width at the midpoint of the shaft, D Transverse depth at the midpoint of the shaft.

CARPO-METACARPUS (Terminology of metacarpus as used by Marples): A Extreme length of second metacarpal, B Extreme length including third metacarpal, C Width one third from the proximal end, D Width two thirds from the proximal end.

PHALANX OF THE MANUS (Proximal phalanx of the second digit): A Length, B Width.

CORACOID: A Total length, B Width of the shaft at the level of the centre of the coracoidal fenestra but excluding the outer rim of the fenestra (i.e. the shaft only), C Total width of the extreme base at the proximal end.

TABLE 4 (cont.)

FEMUR: **A** Length from the hollow between the head and the trochanter at the proximal end to the hollow between the condyles at the distal end, **B** Maximum width at the proximal end, **C** Maximum width at the distal end, **D** Proximo-distal diameter of the head of the femur, **E** Preaxial-postaxial diameter at the midpoint of the shaft, **F** Dorso-ventral diameter at the midpoint of the shaft, **G** Distance from the hollow between the distal condyles to the point where the preaxio-ventral ridge meets the mid-ventral line of the shaft.

TIBIO-TARSUS: **A** Length from the protruberance on the interarticular area to the centre of the furrow between the distal condyles, **B** Maximum width of the distal condyles, **C** Posterior-anterior thickness of the shaft at the midpoint, **D** Internal-external thickness of the shaft at the midpoint.

TARSO-METATARSUS: **A** Length of the second metatarsal from the proximal hollow to the groove on the distal trochlear surface, **B** Length of the third metatarsal from the proximal convexity to the groove on the distal trochlear surface, **C** Length of the fourth metatarsal from the proximal hollow to the groove on the distal trochlear surface, **D** Maximum width at the proximal end, **E** Width of the tarso-metatarsus at the centre, **F** Maximum width at the distal end.

ILIUM-ISCHIUM: **A** Posterior-anterior diameter of the acetabulum, **B** Dorso-ventral diameter of the acetabulum, **C** Length of the ilio-ischiatic fenestra, **D** Width of the ilio-ischiatic fenestra.

SYNSACRUM: **A** Total length, **B** Width taken between the notches of the parapophysis in the region of the sacral vertebrae.

CRANIUM: **A** Width of the skull between the external surfaces of the postorbital processes, **B** Width of the skull between the external surfaces of the suprameatic processes, **C** Depth of the cerebellar dome, **D** Dorso-ventral diameter of the foramen magnum, **E** Transverse diameter of the foramen magnum, **F** Minimum width of the frontal bone between the supraorbital grooves, **G** Distance between the inner surfaces of the exoccipital processes, **H** Anterior-posterior diameter of the basitemporal plate.

E. g. schlereli Humerus

	(No. bones)	A	(No. bones)	B	(No. bones)	C	(No. bones)	D	(No. bones)	E	(No. bones)	F	(No. bones)	G	(No. bones)	H
Finch Cr. (L)	4	73.2-81.0 77.6	10	8.8-10.0 9.1	6	13.2-15.2 14.5	7	15.8-18.0 17.0	6	15.5-17.5 16.8	5	19.5-21.0 20.5	5	22.5-24.1 23.5	5	23.2-26.1 24.9
Recent (L)	9	74.0-78.4 74.9	9	8.9-9.6 9.2	9	12.8-14.6 13.5	9	15.5-17.9 16.5	9	14.9-16.5 15.4	9	19.1-21.3 20.2	9	22.1-25.0 23.8	9	23.6-26.4 25.2
Finch Cr. (R)	14	70.0-82.1 76.7	21	8.5-10.6 9.2	21	13.5-15.1 14.2	16	16.0-18.0 17.0	16	15.8-17.2 16.4	12	19.0-21.0 20.1	14	22.5-24.9 23.1	14	23.9-26.0 24.9
Recent (R)	14	74.0-79.0 76.7	15	8.4-9.4 9.0	14	13.2-15.0 14.0	15	15.8-17.8 16.7	14	15.2-16.7 15.9	14	19.0-21.4 20.5	13	22.5-24.9 23.6	13	24.1-26.0 25.3
Bauer Bay (L)	2	74.5-76.0 75.2	1	9.0	-	(worm)	2	15.5-15.5 15.5	-	(worm)	1	20.5	1	23.2	1	24.0
Bauer Bay (R)	3	74.2-75.0 74.5	1	8.9	3	13.0-13.8 13.4	3	15.5-15.8 15.7	2	14.5-15.1 14.8	3	18.5-19.0 18.7	2	22.0-22.5 22.1	2	23.2-24.0 23.6

TABLE 5: MEASUREMENTS OF BONES

Measurements throughout in mm; L., left, R., right.

TABLE 5 (continued)

E. c. schlegelii Radius

	(No. bones)	A	(No. bones)	B	(No. bones)	C	(No. bones)	D
Finch Cr. (L)	5	51.6-56.0 54.0	5	14.3-15.5 14.8	4	11.7-15.0 13.2	4	4.0-4.2 4.1
Recent (L)	11	52.0-56.3 53.6	11	13.0-14.8 14.0	11	10.5-12.2 11.4	11	3.4-4.0 3.7
Finch Cr. (R)	6	49.7-53.8 52.2	6	13.0-14.7 13.7	6	11.0-12.8 11.7	6	3.0-4.3 3.8
Recent (R)	11	51.5-57.5 54.1	11	13.0-15.0 14.2	11	10.5-12.1 11.5	11	3.4-4.0 3.7
Bauer Bay (L)	1	53.0	1	12.5 (worn)	1	10.5 (worn)	1	3.5 (worn)

E. c. schlegelii Ulna

	(No. bones)	A	(No. bones)	B	(No. bones)	C	(No. bones)	D
Finch Cr. (L)	11	52.2-57.5 55.0	7	17.0-19.0 17.8	7	14.0-15.5 14.8	7	3.5-4.0 3.8
Recent (L)	12	53.5-58.0 55.9	12	15.1-18.8 17.5	12	13.2-16.0 14.5	12	3.1-4.1 3.7
Finch Cr. (R)	8	53.2-57.1 55.1	9	17.1-18.8 17.8	6	14.0-16.2 15.1	8	3.5-4.1 3.9
Recent (R)	10	54.0-58.1 55.9	10	15.5-18.1 17.4	10	13.1-16.0 14.5	10	3.1-4.2 3.7
Bauer Bay	Nil.							

TABLE 5 (continued)

E. c. schlegeli Carpometacarpus

	(No. bones)	A	(No. bones)	B	(No. bones)	C	(No. bones)	D
Finch Cr. (L)	7	42.1-45.0 43.3	8	44.0-47.0 45.3	7	13.4-15.3 14.4	8	15.0-17.0 15.9
Recent (L)	11	41.5-46.0 43.6	11	43.2-48.0 45.5	11	12.3-14.5 13.6	11	13.1-16.5 15.0
Finch Cr. (R)	8	42.0-47.0 43.5	7	44.5-49.1 46.8	8	14.0-15.8 14.5	8	15.0-17.1 15.9
Recent (R)	11	41.6-46.3 43.5	11	43.2-48.2 45.6	11	12.3-15.0 13.7	11	13.1-16.2 15.1
Bauer Bay	Nil.							

E. c. schlegeli. Phalanx of the Manus = proximal phalanx of second digit.

	(No. bones)	A	(No. bones)	B
Finch Cr.	9	26.8-31.5 29.1	9	9.6-10.8 10.2
Recent	9	28.8-30.5 29.7	9	10.0-10.5 10.2
Bauer Bay	Nil.			

TABLE 5 (continued)

E. c. schlegelii Coracoid.

	(No. bones)	A	(No. bones)	B	(No. bones)	C
Finch Cr. (L)	13	81.9-88.0 84.1	16	10.0-11.5 10.6	5	27.1-31.0 28.6
Recent (L)	12	84.7-90.9 87.5	12	9.8-11.0 10.4	12	27.0-30.4 28.8
Finch Cr. (P)	14	80.9-91.5 86.9	16	9.9-11.9 10.9	6	27.0-30.5 28.2
Recent (R)	10	85.0-90.0 87.7	10	9.6-10.9 10.3	10	26.9-30.8 28.6
Bauer Bay (L)	1	86.0	1	11.5	-	-
Bauer Bay (R)	3	80.5-88.9 83.4	2	9.2-11.0 10.1	1	28.5

E. c. schlegelii. Femur.

	(No. bones)	A	(No. bones)	B	(No. bones)	C	(No. bones)	D	(No. bones)	E	(No. bones)	F	(No. bones)	G
Finch Cr. (L)	15	70.6-76.5 73.4	13	17.0-18.9 17.5	14	15.0-16.0 15.5	13	8.2-9.9 9.0	17	7.2-8.2 7.9	17	7.9-9.2 8.5	12	30.0-36.5 31.9
Recent (L)	12	70.3-75.2 73.3	12	16.1-18.6 17.5	12	14.8-16.9 16.0	12	8.2-10.3 9.1	12	7.0-8.2 7.8	12	7.6-9.5 8.4	12	29.8-34.6 32.1
Finch Cr. (R)	18	70.0-77.0 73.4	14	16.0-18.0 17.0	15	14.8-16.5 15.5	16	8.5-10.0 9.1	17	7.0-8.7 7.4	15	7.8-8.9 8.5	10	30.5-35.0 32.6
Recent (R)	9	70.5-75.4 73.4	9	16.3-18.2 17.5	9	14.5-16.5 15.8	9	8.2-10.1 9.2	9	7.1-8.3 7.9	9	7.9-9.2 8.5	9	29.1-34.9 31.7
Bauer Bay (L)	1	77.1	1	16.9	1	16.0	-	-	1	8.0	1	8.8	1	33.0
Bauer Bay (R)	1	76.0	1	18.0	1	16.8	-	-	1	7.5	1	8.0	1	33.5

TABLE 5 (continued)

C

<u>A. patagonica.</u> Humerus																
	(No. bones)	A	(No. bones)	B	(No. bones)	C	(No. bones)	D	(No. bones)	E	(No. bones)	F	(No. bones)	G	(No. bones)	H
Finch Cr. (L) Nil.....																
Recent (L)	7	106.2-112.0 108.4	8	12.0-13.0 12.3	8	18.0-20.5 18.5	8	20.9-24.0 22.3	8	19.8-22.0 20.5	5	26.0-29.0 27.0	5	29.0-31.5 29.9	5	31.0-34.0 32.1
Finch Cr. (R)	1	105.0	2	12.5-13.0 12.8	2	18.7-18.8 18.8	2	22.9-23.0 23.0	2	21.0-21.2 21.1	1	26.5	1	29.7	1	31.9
Recent (R)	5	106.8-116.5 111.8	9	11.7-13.0 12.1	9	18.0-20.5 18.9	9	21.5-24.4 23.0	9	19.3-22.5 20.7	5	26.8-29.0 27.5	5	30.2-31.5 30.7	5	31.8-34.0 32.5
Bauer Bay (L) Nil...																
Bauer Bay (R)	2	106.5-108.0 107.2	1	12.0	3	18.2-19.0 18.7	2	22.5-23.0 22.7	3	20.5-21.5 20.8	1	27.1	1	29.6	1	32.0

<u>A. patagonica.</u> Carpometacarpus.									
	(No. bones)	A	(No. bones)	B	(No. bones)	C	(No. bones)	D	(No. bones)
Finch Creek (L) Nil									
Recent (L)	6	62.0-66.2 64.2	6	64.6-68.5 66.5	5	17.0-20.0 17.8	5	17.9-20.5 18.4	
Finch Cr. (R)	1	63.7	1	66.0	1	18.2	1	19.0	
Recent (R)	2	62.0-64.5 63.2	2	64.5-66.0 65.2	2	17.5-20.0 18.7	2	18.1-20.5 19.3	
Bauer Bay Nil.									

TABLE 5 (continued)

A. patagonica. Coracoid

	(No. bones)	A	(No. bones)	B	(No. bones)	C
Finch Creek (L)	Nil.....					
Recent (L)	Nil.....					
Finch Creek (R)	Nil.....					
Recent (R)	3	124.0-127.0 125.0	3	14.2-15.0 14.5	3	38.0-40.0 39.2
Bauer Bay (L)	1	127.0	2	15.0-15.0 15.0	2	35.0-39.5 37.2
Bauer Bay (R)	-	--	-	--	1	36.5

A. patagonica. Femur

	(No. bones)	A	(No. bones)	B	(No. bones)	C	(No. bones)	D	(No. bones)	E	(No. bones)	F
Finch Cr. (L) Nil...												
Recent (L)	3	88.0-89.0 88.6	3	23.2-25.5 24.0	3	23.0-25.5 23.9	3	12.0-12.5 12.2	2	10.9-12.5 11.7	2	12.2-13.5 12.8
Finch Cr. (R)	1	83.0	1	23.5	1	23.0	1	12.6	1	11.1	1	11.6
Recent (R)	6	83.0-91.5 86.6	4	23.6-25.5 24.5	5	22.7-25.5 23.6	4	12.0-12.5 12.2	6	10.1-12.2 10.6	6	11.5-13.5 12.2
Bauer Bay (L)	1	90.1	2	23.5-24.5 24.0	2	23.3-25.0 24.1	1	12.5	4	10.8-11.5 11.1	4	12.0-13.5 12.7
Bauer Bay (R)	2	89.0-90.0 89.5	1	25.1	4	23.5-25.5 24.6	1	12.5	1	11.4	1	13.0

A. patagonica Tibiotarsus.

	(No. bones)	A	(No. bones)	B	(No. bones)	C	(No. bones)	D
Finch Creek (L) Nil...								
Recent (L)	3	156.0-165.0 161.6	4	21.5-24.0 22.2	4	9.0-10.6 9.6	4	10.1-12.2 10.8
Finch Creek (R)	-	--	1	22.2	-	--	-	--
Recent (R)	7	160.0-171.5 164.7	5	21.0-24.0 22.1	7	9.0-10.6 9.6	7	10.5-12.8 11.3
Bauer Bay (L)	-	--	2	23.1-23.1 23.1	-	--	-	--
Bauer Bay (R)	-	--	4	22.9-24.0 23.7	1	10.5	1	11.6

TABLE 6
MEANS AND VARIANCES OF SELECTED MEASUREMENTS

<i>E. c. schlegeli</i>				
	Sample size	Mean	Variance	Comparison of variances
HUMERUS				
Measurement A				Variances significantly different at 1% level
Finch Creek	18	76.8	9.69	
Bauer Bay	5	74.8	0.503	
Recent	19	76.0	1.92	
Measurement D				Variances significantly different at 5% level
Finch Creek	23	17.0	0.436	
Bauer Bay	5	15.6	0.026	
Recent	19	16.5	0.490	
RADIUS				
Measurement A				
Finch Creek	11	53.0	3.70	
Recent	22	53.9	2.92	
Measurement B				
Finch Creek	11	14.2	0.659	
Recent	22	14.1	0.315	
ULNA				
Measurement A				
Finch Creek	19	55.0	3.33	
Recent	22	55.9	2.35	
Measurement B				
Finch Creek	16	17.8	0.350	
Recent	22	17.5	0.795	
CARPO-METACARPUS				
Measurement B				
Finch Creek	15	45.6	2.12	
Recent	22	45.6	2.74	
Measurement D				
Finch Creek	16	15.9	0.437	
Recent	22	15.1	0.918	
CORACOID				
Measurement A				Variances significantly different at 5% level
Finch Creek	27	85.6	9.14	
Recent	22	87.6	2.64	
Measurement C				
Finch Creek	11	28.4	1.73	
Recent	22	28.8	1.61	
FEMUR				
Measurement A				
Finch Creek	33	73.2	3.57	
Recent	21	73.4	1.92	
Measurement B				
Finch Creek	27	17.3	0.377	
Recent	21	17.6	0.432	
TIBIO-TARSUS				
Measurement A				
Finch Creek	19	118.6	7.34	
Recent	14	120.5	9.39	
Measurement B				
Finch Creek	20	14.4	0.308	
Recent	14	14.8	0.221	
TARSO-METATARSUS				
Measurement B				Variances significantly different at 5% level
Finch Creek	15	29.6	0.692	
Recent	18	30.2	2.49	

TABLE 6 (continued)

<i>E. c. schlegeli</i>				
	Sample size	Mean	Variance	Comparison of variances
Measurement E				
Finch Creek	13	16.5	0.504	
Recent	18	15.8	0.438	
ILIUM-ISCHIUM				
Measurement A				
Finch Creek	22	11.2	0.227	
Recent	20	11.4	0.392	
Measurement B				
Finch Creek	21	11.7	0.262	
Recent	20	11.1	0.497	
SYNSACRUM				
Measurement A				
Finch Creek	4	90.0	13.5	
Recent	11	89.7	37.0	
Measurement B				
Finch Creek	19	14.8	0.432	
Recent	12	14.8	0.454	
CRANIUM				
Measurement A				
Finch Creek	7	52.5	1.49	
Recent	8	52.6	2.95	
Measurement C				
Finch Creek	10	20.8	1.90	
Recent	7	22.7	1.90	
<i>Aptenodytes patagonica</i>				
	Sample size	Mean	Variance	Comparison of variances
HUMERUS				
Measurement A				
Recent	12	109.8	12.97	
Measurement D				
Recent	17	22.7	1.32	
FEMUR				
Measurement A				
Recent	9	87.3	6.85	
Measurement B				
Recent	7	24.3	0.990	
CARPO-METACARPUS				
Measurement B				
Recent	8	66.2	2.00	
Measurement D				
Recent	7	18.7	1.52	
TIBIO-TARSUS				
Measurement A				
Recent	10	163.8	20.8	
Measurement B				
Bauer Bay	6	23.5	0.286	
Recent	9	22.1	1.27	

Variance (s^2) is the square of the standard deviation (s). Samples include both right and left bones.

TABLE 7
ANALYSIS OF BAUER BAY SOIL SAMPLES

Sample	Md	Q3	Q1	P90	P10	So	Sk	K
A1	0.49	0.62	0.40	0.74	0.34	1.24	1.03	0.37
B2	0.49	0.56	0.42	0.67	0.33	1.15	0.98	0.21
C1	0.49	0.64	0.38	0.82	0.31	1.30	1.02	0.25
C2	0.45	0.53	0.38	0.66	0.32	1.18	0.99	0.22
C3	0.53	0.66	0.42	0.80	0.36	1.25	0.99	0.27
D3	0.49	0.62	0.40	0.72	0.33	1.24	1.03	0.28
D5	0.46	0.58	0.37	0.67	0.30	1.25	1.02	0.27
D6	0.45	0.58	0.38	0.68	0.32	1.24	1.09	0.28
E1	0.45	0.55	0.37	0.66	0.30	1.22	1.01	0.25
F	0.30	0.35	0.25	0.44	0.21	1.18	0.98	0.22
G	0.45	0.57	0.36	0.69	0.24	1.26	1.01	0.23
Bauer Beach	0.29	0.35	0.24	0.42	0.22	1.20	1.00	0.27

Md, median diameter in mm. Q3 and Q1, diameters associated with quartiles. P90 and P10, diameters associated with the 10 and 90 percentile measures. So, sorting = $\frac{Q3}{Q1}$ and is a measure of the spread of the distribution. Values less than 2.5 are well sorted. Sk, skewness = $\frac{Q1 - Q3}{(Md)^2}$ is a measure of the symmetry of distribution. A value of 1 represents a perfectly symmetrical distribution. K, kurtosis = $\frac{Q3 - Q1}{2(P90 - P10)}$ is not clearly understood, but provides a measure of the quantity in the maximum plus range for a unimodal distribution.

APPENDIX

GEOLOGY OF FOSSIL PENGUIN BEDS, MACQUARIE ISLAND

By

EDMUND D. GILL

Macquarie Island is the subaerial projection of an elongate sub-oceanic ridge which is of similar proportions and orientation, but many times the size (Summerhayes 1967a, Cullen 1970). This Macquarie Ridge is a linear extension of the New Zealand submarine plateau, and is commonly regarded as an island arc system (Cullen 1967, Summerhayes 1967b, Varne, Gee & Quilty 1969, Houtz, Ewing & Embley 1971). It has been suggested that Macquarie Island is 'ocean floor on land', a segment of Pliocene oceanic crust emerged from the ocean (Anonymous 1969). That Macquarie Island is sited on a platform is important (for the present purpose) because part at least of this would have been bared during the Last Glaciation by eustatic drop in sealevel, so changing the outline and extent of the island.

Although it is a Sub-Antarctic island, Macquarie Island does not accumulate ice under present conditions because it is long and narrow, and stands in an area of high winds. The snow is blown away, and insufficient accumulates to allow

an ice cap to form. For the same reason it could not have formed an ice cap of sufficient magnitude to cause detectable isostatic depression in the Last Glacial. This simplifies the interpretation of the Fossil Penguin beds in that no complications from isostasy are present.

SEDIMENTOLOGY

Finch Creek flows into Sandy Bay (note name) on the east side of Macquarie Island, and its mouth is accordant with present sealevel. It has incised at least 9 m through a deposit of well-stratified, lightly compacted postglacial sediment which has the surface characteristics of a more or less flat floodplain terrace. A basal gravel and sand is followed by peaty mud, and this cycle is repeated three times with a topmost bed of sand and gravel (Mawson 1943, p. 83). Another section shown by Mawson has disturbed beds. The succession indicates a sharp alteration in the dynamics of deposition. Only a turbulent stream flowing over a short floodplain from a steep terrain could deposit the ill-sorted sands and the gravels which include quite large pebbles. On the other hand, only still waters could deposit the peaty muds. The suite of sediments appears from the photographs to be fluvial, or fluvial and lacustrine, but not fluvioglacial as suggested in the literature.

PROVENANCE OF FOSSILS

The penguin bones are well preserved. The photographs show that the bones are not lying parallel to the bedding planes, but as a group are rather randomly oriented, with angles up to 50°. In a peaty mud facies, bones cannot be transported as the dynamics are too low, nor can they be deposited at such angles. In the sand-gravel facies, however, both these processes are normal. Where bones occur in the mud facies they are either intrusive or repositioned due to bioturbation caused by the activities of other animals. There is need for the careful examination of the upper silty peat laminations to ascertain which is the case at Macquarie Island.

CHRONOLOGY

While only one horizon (c.6 m above creek and sealevel) is dated in the Finch Creek deposit (6100 ± 120 y. B.P., GaK-643) and one horizon at Bauer Bay (3980 ± 140 y. B.P., GaK-644), these datings nevertheless indicate mid-Holocene age. However, these datings were made on bones wherein contamination can occur. Also, there are isotopic problems with dating at these high latitudes, and as there is no supporting net of dates on the island, they should not be taken as necessarily precise. It would be worthwhile to date a series of samples through the Finch Creek beds as well as to examine carefully the fabric of the various strata. At the same time as dating the various organic fractions present, the proportions of the various isotopes of carbon in the local environment must be ascertained. The Bauer Bay Beds offer an obvious extension of such a programme. We can infer, however, that the valley in which the Finch Creek Beds are emplaced is older than mid-Holocene, which is the age of at least some of the sediments.

At least three sedimentary cycles of sand-gravel and mud occurred, so there must have been an intermittent barrier in the creek that grossly changed the dynamics of the stream waters at the site. The mid-Holocene Thermal Maximum extended from 6000 years ago or

earlier to about 4000 years ago, and was a time of slightly higher world temperatures. Such would perhaps result in a more intense and less protracted seasonal melt and consequent runoff on Macquarie Island. The island's marked tendency to mass movement on steep slopes would be accentuated at such times, and hillsides may have temporarily dammed the creek, permitting peaty mud to be deposited behind the barrier. Another and more likely possibility is the growth of a berm-top sand dune at Sandy Bay where the present-day wave-built berm frequently dams Finch Creek. Such a dune could dam Finch Creek intermittently, and so allow the stillwater sediments to accumulate. The absence of such a dune today is perfectly consistent with the marked destruction suffered by the massive dunes at Bauer Bay.

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EXPLANATION OF PLATES

PLATE 8

Figs. 1-2—Finch Creek environs showing extent of beds excluding E. extension. The far right paper marker in Fig. 1 is the far left paper marker in Fig. 2. Penguins are shown on the penguin-path. The worker is at the western extension, i.e. 2 W. Fig. 4 shows Blake's section enlarged and Vestjens' upper exposure indicated by paper markers at right. The stake used as a datum point is just visible on bank directly above the ladder; Fig. 3 shows fossil bones *in situ*, stratum 2 W. Photographs 1 & 2 by A. R. McEvey, 3 & 4 by W. J. M. Vestjens.

PLATE 9

Fossil and recent bones of *E. c. schlegeli**Tarso-metatarsus*

Fig. 1, Finch Cr., R., ventral aspect, B9660 (1), $\times 1.05$; Fig. 2, Recent, R., ventral aspect, B7867, $\times 1.05$; Fig. 3, Finch Cr., L., ventral aspect, B9647 (6), $\times 1.05$; Fig. 4, Recent, L., ventral aspect, B7886, $\times 1.05$ (showing two pairs of matching size).

Humerus

Fig. 5, Finch Cr., R., ventral aspect showing scar of insertion of *M. pectoralis primus*, B9644 (11), $\times .95$; Fig. 6, Recent, R., ventral aspect, B7868, $\times .95$; Fig. 7, Finch Cr., R., dorsal aspect, B9644 (11) $\times 0.95$; Fig. 8, Recent, R., dorsal aspect, B7868, $\times 0.95$.

Radius

Fig. 9, Finch Cr., L., ventral aspect, B9661 (3), $\times 0.8$; Fig. 10, Recent, R., dorsal aspect, B7865, $\times 0.8$.

Ulna

Fig. 11, Finch Cr., R., ventral aspect, B9662 (1), $\times 0.8$; Fig. 12, Recent, R., ventral aspect, B7867, $\times 0.8$; Fig. 13, Finch Cr., L., dorsal aspect, B9649 (4), $\times 0.8$; Fig. 14, Recent, L., dorsal aspect, B7868, $\times 0.8$.

Carpo-metacarpus

Fig. 15, Finch Cr., L., dorsal aspect, B9650 (4), $\times 1.1$; Fig. 16, Recent, L., dorsal aspect, B7868, $\times 1.2$; Fig. 17, Finch Cr., R., ventral aspect, B9650 (9), $\times 1.1$; Fig. 18, Recent, R., ventral aspect, B7866, $\times 1.2$.

Coracoid

Fig. 19, Finch Cr., R., dorsal aspect, B9653 (6), $\times 0.95$; Fig. 20, Recent, R., dorsal aspect, B7868, $\times 0.95$; Fig. 21, as Fig. 19, ventral aspect, $\times 0.95$; Fig. 22, as Fig. 20, ventral aspect, $\times 0.95$.

PLATE 10

Fossil and recent bones of *E. c. schlegeli**Synsacrum*

Fig. 23, Finch Cr., ventral aspect, B9655 (2), $\times 0.8$; Fig. 24, Recent, ventral aspect, B7869, $\times 0.8$.

Femur

Fig. 25, Finch Cr., R., ventral aspect, B9658 (3), $\times 0.95$; Fig. 26, Recent, R., ventral aspect, B7868, $\times 0.95$.

Cranium

Fig. 27, Finch Cr., dorsal aspect, B9667 (1), $\times 0.7$; Fig. 28, Recent, dorsal aspect, W5654, $\times 0.7$.

Sternum

Fig. 29, Recent, anterior aspect, $\times 0.9$; Fig. 30, Finch Cr., anterior aspect, B9664 (1), $\times 0.9$.

Ilium-Ischium

Fig. 31, Finch Cr., R., internal aspect, B9656 (6), $\times 0.8$; Fig. 32, Recent, R., internal aspect, B7869, $\times 0.8$.

Scapula

Fig. 33, Finch Cr., R., dorsal aspect, B9670 (7), $\times 0.8$; Fig. 34, Finch Cr., R., ventral aspect, B9670 (3), $\times 0.8$; Fig. 35, Recent, R., dorsal aspect, W5655, $\times 0.8$.

Clavicle

Fig. 36, Finch Cr., L., external aspect, B9652 (9), $\times 0.8$; Fig. 37, Finch Cr., L., external aspect, B9652 (2), $\times 0.8$; Fig. 38, Recent, L. & R., external aspect, B7868, $\times 0.8$.

PLATE 11

Fossil and recent bones of *E. c. schlegeli* and *A. patagonica**E. c. schlegeli**Sternum*

Fig. 39, Finch Cr., L., lateral aspect, B9664 (5), $\times 0.7$; Fig. 40, Recent, L., lateral aspect, $\times 0.7$.

Tibio-tarsus

Fig. 41, Finch Cr., L., lateral aspect, B9646 (12), $\times 0.7$; Fig. 42, Recent, L., lateral aspect, B7868, $\times 0.7$.

*Aptenodytes patagonica**Humerus*

Fig. 43, Bauer Bay, R., ventral aspect, B10600 (1), $\times 1.05$; Fig. 44, Finch Cr., R., ventral aspect, B10595 (2), $\times 1.05$; Fig. 45, Recent, R., ventral aspect, B4356, $\times 1$.

Femur

Fig. 46, Finch Cr., R., ventral aspect, B10598 (1), $\times 1.2$; Fig. 47, Bauer Bay, R., ventral aspect, B10607 (2), $\times 1.2$; Fig. 48, Recent, R., ventral aspect, B4356, $\times 1.2$. Photographs 43-48 by I. Roper.









THE VICTORIAN ISOGRAPTIDS AND ISOGRAPTID-LIKE GRAPTOLOIDS

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ABSTRACT: The work of W. J. Harris on the Family Isograptidae Harris is reviewed, together with subsequent studies by others, notably Bulman and Skevington. A study is made of the proximal development, thecae, and rhabdosomal morphology of species included by Harris in the Family Isograptidae. The Family is reduced in status to a Sub-family, Isograptinae, in the Family Dichograptidae Lapworth. The genera *Oncograptus* and *Cardiograptus* are transferred to the Sub-family Cardio-graptinae Mu and Zhan, and *Skiagraptus* to the Family Dichograptidae Lapworth. The status of *Maeandrograptus* is tentatively referred to the Family Sinograptidae Mu. The status of the numerous varieties of *Isograptus caduceus* is raised to the specific level.

The range of the isograptids in the Ordovician rocks of Victoria is considered and the retention of the term Isograptid Fauna is argued to be justified since the isograptids and isograptid-like species form an important unit in the Lower Ordovician rocks in Victoria.

The development and evolution of the isograptids is discussed and it is shown that while certain of the evolutionary trends postulated by Harris can be substantiated, others are found to be invalid on either, or both, palaeontological and stratigraphic evidence.

Finally, formal description of all the isograptid and isograptid-like species in Victoria are presented. In this section it is argued that *Isograptus caduceus* var. *victoriae* Harris and *Isograptus gibberulus* Nicholson are conspecific.

CONTENTS

INTRODUCTION	Page 176
INTRODUCTORY NOTE ON ISOGRAPTID CLASSIFICATION	177
DEVELOPMENT OF THE PROXIMAL REGION IN ISOGRAPTIDS AND ISOGRAPTID-LIKE RHABDOSOMES	178
THECAL TYPES IN ISOGRAPTIDS	180
RHABDOSOMAL CHARACTERISTICS OF THE ISOGRAPTIDS	184
A REVISED CLASSIFICATION OF THE ISOGRAPTIDS	186
STRATIGRAPHIC ASPECTS OF THE ISOGRAPTIDS IN VICTORIA	188
DEVELOPMENT AND EVOLUTION OF THE ISOGRAPTIDS	188
SYSTEMATIC PALAEONTOLOGY	191
Genus <i>Didymograptus</i> McCoy	191
Genus <i>Skiagraptus</i> Harris	193
Genus <i>Isograptus</i> Moberg	193
Genus <i>Oncograptus</i> T. S. Hall	205
Genus <i>Cardiograptus</i> Harris and Keble	208
Genus <i>Pseudisograptus</i> Beavis	209
Genus <i>Maeandrograptus</i> Moberg	212
CONCLUSIONS	212
REFERENCES	213

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INTRODUCTION

In 1933 W. J. Harris published his important work '*Isograptus caduceus* and its allies in Victoria.' He was aware of the limitations imposed on his work by the highly compressed state of preservation of the material available to him, and he anticipated a considerable revision of his ideas as more detailed studies on uncompressed material were completed. The results of Bulman's (1932b) work on Scandinavian graptolites were fully utilized by Harris and formed the basis for the major part of his taxonomic work.

On the basis of, particularly, the type of growth in the initial stages of the rhabdosome, Harris created a new family, the Isograptidae in which he included the genera *Isograptus* Moberg, *Maeandrograptus* Moberg, *Oncograptus* T. S. Hall, *Skiagraptus* Harris and *Cardiograptus* Harris and Keble. On the evidence available, Harris assumed that all species of these genera had the same type of proximal development as *Isograptus gibberulus*, determined for this species by Elles (1922), and defined by Bulman (1932a) as the Isograptid Type. Harris clearly believed, though he did not argue his case, that *Isograptus caduceus* and *Isograptus gibberulus* were conspecific.

Apart from the same type of proximal development, Harris considered that unity was given to the Family Isograptidae by progressive development along three lines (1933, pp. 85-86):

- (i) the rhabdosome becomes increasingly scandent;
- (ii) there is a progression, and then a regression, in the form of thecal apertures;
- (iii) an increasing tendency towards concrescence 'which may be regarded as the chief basis for the Family.'

Harris could find no evidence to indicate the origin of the isograptids. However, he postulated three lines of development within the Family showing a number of evolutionary trends:

- (i) A progressive increase in:
 - (a) the size of the rhabdosome, with a more open spacing of thecae;
 - (b) angle of divergence;
 - (c) downward direction of denticles;
 - (d) completeness of thecal overlap.
- (ii) A development into allied genera marked by:
 - (a) a reduction in size;
 - (b) an increase in angle of divergence leading to diploleural biserial forms;
 - (c) variation in denticles;
 - (d) reduction in thecal overlap: the manubriate species;
 - (e) grouping of thecal origins in the sicular region, as distinct from concrescence,

but occurring with concrescence in *Oncograptus* and *Cardiograptus*.

- (iii) The extinction of the Family except for rare forms.

The first revision of Harris's ideas came with the publication by Bulman (1936b) of evidence to show that the proximal development of *Oncograptus* was a dichograptid type, and much more primitive than that of any isograptid; he postulated derivation of *Oncograptus* from an ancestral *Tetragraptus*, independently of *Isograptus*. Mu and Lee (1958) agreed with Bulman's results, although later, Mu and Zhan (1966) claimed that Chinese material tended to support the original views of Harris on the development of *Oncograptus*.

In 1968, Skevington referred *Isograptus manubriatus* to the genus *Maeandrograptus*, which he included in the Family Sinograptidae Mu, largely on the basis of thecal morphology, notably the development of protheceal folds. He rejected as invalid the families Isograptidae Harris and Cardiograptidae Mu and Zhan. He regarded *Oncograptus* and *Cardiograptus morsus* as variants of his '*Maeandrograptus manubriatus*,' and *Skiagraptus* as a 'form genus' to which he referred *Cardiograptus crawfordi*. Bulman (1968) described the proximal development of an example of *Isograptus manubriatus* showing this to be a considerably modified isograptid type. In 1969, Whittington and Rickards described the proximal end of *Skiagraptus* showing this to be a modified dichograptid type, with an incipient monopleural arrangement of the thecae. This genus was referred by these workers to the Family Dichograptidae Lapworth.

Finally, Beavis (1972) discussed *Isograptus manubriatus* and showed that there is no justification for this species to be regarded as a maeandrograptid: at the same time, the species showed significant departures from the typical *Isograptus*, and a new genus *Pseudisograptus* Beavis was introduced to which were referred the three manubriate species: *I. manubriatus*, *I. hastatus*, and *I. dumosus*.

Since its publication in 1933, Harris's work has been subject to considerable revision, and this has been based particularly on proximal development of the rhabdosome. This present paper presents the results of the writers' research on this group of graptolites. Much of the work has been based on the compressed Victorian material, and preparation of the paper was deferred until the better preserved European and American material could be studied.

The final stages of the work, and the preparation of the paper were carried out at the Sedgwick Museum, University of Cambridge, during

a year's leave from the University of Melbourne. The work was undertaken at the suggestion of the late Dr. W. J. Harris. We are indebted to Professor O. M. B. Bulman for helpful discussion and criticism, to Professor H. B. Whittington for facilities, discussion and for his making available isolated specimens of *Skiagraptus* described by him and by Dr. R. B. Rickards. To Dr. Rickards and Professor Bulman we are indebted for their detailed criticism of the section of the work on the manubriate species.

In this paper, the following abbreviations are used—SM: Sedgwick Museum, University of Cambridge; NV: National Museum of Victoria; GV: Geological Survey of Victoria; GS: Geology School, University of Melbourne.

INTRODUCTORY NOTE ON ISOGRAPTID CLASSIFICATION

Although Harris accepted the ideas of Nicholson and Marr (1895) and of Elles (1898) that thecal characters are the most important criterion for familial separation, he appears to have regarded the type of proximal development of the rhabdosome as being of at least equal, if not greater, importance. He also accepted the conclusion of these earlier workers that such criteria as thecal spacing, thecal overlap, and apertural angle, were of genetic origin and of importance in generic distinction. Although he used these criteria, he pointed out that they are difficult, if not impossible, to distinguish in the Victorian material because of the compressed state of preservation.

Bulman (1963) discussed the basis for the classification of graptolites in general, showing that these organisms present two sets of separate characters: those of the rhabdosome as a whole, and those of the thecae. Changes in rhabdosomal form he indicated to be abrupt and irregular and taxonomic units based on these are precise and readily defined. The changes are astogenic, and taxa based on them may not be biologically valid. Bulman regarded thecal characters as a sounder basis for biological classification. In an earlier work (Bulman, 1955) he included the isograptids in the Family Dichograptidae, but in his 1963 paper, he remarked that 'some subdivision of this family has been proposed (e.g. Isograptidae Harris 1933, Sinograptidae Mu 1957) and is probably desirable at the Sub-family level.'

The Family Sinograptidae was introduced by Mu in 1957 to include some Chinese and European genera: *Allograptus* Mu, *Holmograptus* Kozłowski, *Tylograptus* Mu and *Sinograptus* Mu. This Family was extended by Jaanusson (1964) to in-

clude genera which do not necessarily have a dichograptid type proximal development but which were characterized by folding of the prothecae. The amended Family included *Meandrogaptus* Moberg, *Oslograptus* Jaanusson and *Cymatograptus* Jaanusson in addition to the genera included by Mu.

Mu and Zhan (1966) proposed the Family Cardiograptidae to include the genera *Cardiograptus* Harris and Keble, *Paracardiograptus* Mu and Lee and *Skiagraptus* Harris. No formal diagnosis of the Family was published (at least in English), but the main characteristics are:

- (i) the rhabdosome is two-stiped, usually with a well developed virgula;
- (ii) the thecae have a dipleurial arrangement;
- (iii) the stipes are scandent.

In this paper (p. 186), a revised classification of the Victorian isograptids and isograptid-like forms is submitted. The original classification proposed by Harris was:

Order GRAPTOLOIDEA Lapworth 1875

Family DICHOGRAPTIDAE Lapworth 1873

Genus *Didymograptus* McCoy 1851

Didymograptus eocaduceus Harris

Didymograptus hemicyclus Harris

Family ISOGRAPTIDAE Harris 1933

Genus *Isograptus* Moberg 1892

Isograptus caduceus (Salter) et vars. Harris

Isograptus forcipiformis Ruedemann

Isograptus hastatus Harris

Isograptus manubriatus (T. S. Hall)

Isograptus dumosus Harris

Isograptus ovatus (T. S. Hall)

Genus *Oncograptus* T. S. Hall 1915

Oncograptus upsilon T. S. Hall

Oncograptus upsilon biangulatus Harris and Keble

Genus *Cardiograptus* Harris and Keble 1916

Cardiograptus morsus Harris and Keble

Cardiograptus crawfordi Harris

Genus *Skiagraptus* Harris 1933

Skiagraptus gnomonicus Harris and Keble

Genus *Maeandrogaptus* Moberg 1892

Maeandrogaptus aggestus Harris

Maeandrogaptus iau Harris

Harris recognized the following varieties of *Isograptus caduceus*: *primula*, *lunata*, *victoriae* (forma typica), *maximus*, *maximodivergens*, *divergens*, *pertensa*, *imitata* and *tenuis*. The var. *horrida* is certainly a small form of *pertensa*. He

considered two other possible varieties; *spinifer* and *expansa*, but concluded that they did not show sufficiently distinctive characters to warrant such recognition. All of these varieties were figured by Harris, but no formal descriptions were published.

DEVELOPMENT OF THE PROXIMAL REGION IN ISOGRAPTID AND ISOGRAPTID-LIKE RHABDOSOMES

At the time of the publication of his paper, Harris (1933) had available information on the proximal development of *Isograptus gibberulus* and *Maeandrograptus schmalensei*. Since that time, details of the proximal development of *Oncograptus upsilon biangulatus* (Bulman, 1936b), *Isograptus manubriatus* (Bulman, 1968) *Maeandrograptus? geniculatus* (Skevington, 1965) and *Skiagraptus* sp. (Whittington and Rickards, 1969) have been determined from well preserved material. At the present time, information is available relating to the proximal development of at least one species of each genus included by Harris in the family Isograptidae, with the exception of *Cardiograptus*.

Isograptus gibberulus

The proximal development of this species was described by Elles (1898), Törnquist (1901), and Elles and Wood (1901). Elles (1922) apparently did not regard the development of this species as

a distinct type, but she stated that *Isograptus gibberulus* 'showed the beginning of a structure characteristic of a more advanced type of development.' Bulman (1932a, 1932b, 1936a) formally defined the 'Isograptid type of development' in which $th1^2$, and not $th1^1$, was the dicalycal theca. *I. gibberulus* shows the 'gibberulus stage of this type of development, with $th2^1$ developing somewhat lower down on $th1^2$ than in the more advanced *hirundo* stage, so that the crossing canal is more conspicuous.' Bulman (1932b) regarded the type of development as the most important characteristic, but he qualified this assertion by stating that since so little was known of other species of *Isograptus*, it remained uncertain as to which features were of generic importance.

In an isolated specimen from Killeröd, Sweden (SM No. A 513512) $th1^1$ arises very high up on the sicula (almost certainly the prosicula) and grows downward for its full length in contact with the sicula (Fig. 1a). $Th1^2$ arises about 0.6 mm below the bud of $th1^1$ (Fig. 1b). The second crossing canal is not clear in this specimen, but $th2^1$ appears to arise high up on $th1^2$.

The compressed Victorian material gives no evidence of the true nature of the proximal development, although in some examples (c.g. SM No. A 60286) the budding of $th1^1$ in the apical region of the sicula can be seen quite clearly. We must agree with Harris that, without the know-

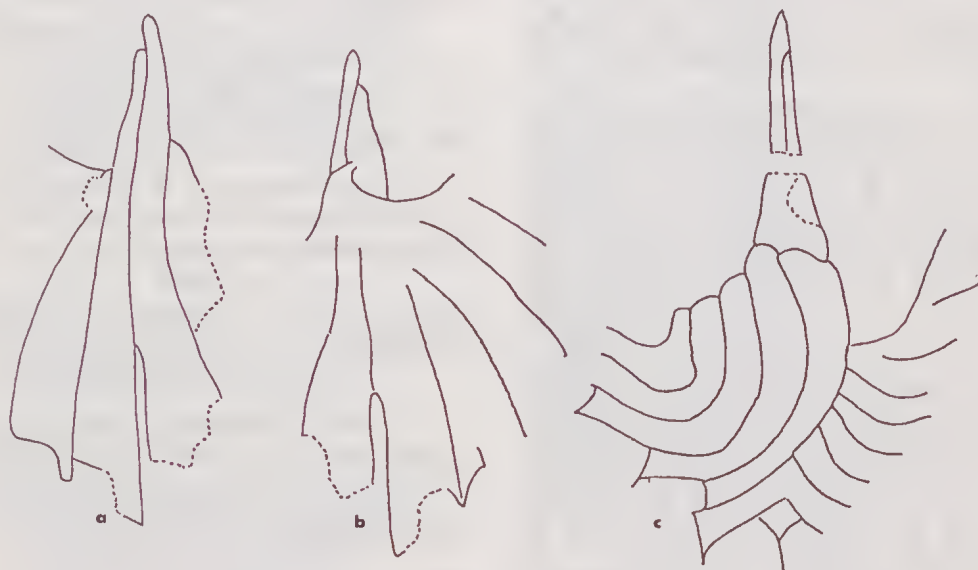


FIG. 1—(a) *Isograptus gibberulus* SM A513152 Lower *Didymograptus* Shales, Killeröd, Sweden, obverse aspect, $\times 12.5$. (b) Same specimen as (a), reverse aspect, $\times 12.5$. (c) *Pseudisograptus manubriatus* SM A603142 proximal end. Fort Pena Formation, Marathon, Texas, U.S.A. Latex mould, $\times 12.5$, figured by Bulman (1968).

ledge from the uncompressed European material the data from the Victorian would be difficult, if not impossible, to interpret.

Pseudisograptus manubriatus

Harris implied that he did not understand fully the relationship between the manubriate, and the 'normal' species of *Isograptus*; he was prepared to assume, however, on the evidence available, that the proximal development of '*Isograptus*' *manubriatus* was isograptid, but of a special type. His figures 1a to 1e of Plate VI (1933) indicate that he was justified in his assumption, especially if he regarded as the main feature of the isograptid type of development that $th1^2$ was dialycal, and this we believe he did. In 1968, Bulman described the development of a specimen of this species from Marathon, Texas (SM No. A 603142) which has been re-examined by the present writers. This species has, like other isograptids, a proximal development which is fundamentally platycalycal, i.e. $th1^2$ crosses $th1^1$ and the sicula by a crossing canal on the reverse side, leaving the sicula free on the obverse side. It does, however, simulate a pericalycal style in that the proximal portions of $th4^1$ to $th6^1$ seem to originate on the obverse side, and seem to cover, or enclose, some part of the sicula.

The sicula is long and narrow, and $th1^1$ buds high up on the sicula, but whether on the prosicula, as in *Isograptus gibberulus* is not clear. $Th1^1$ grows down along the sicula, and in contact with it until close to the apertural region, when it turns outwards. The origin of $th1^2$ is obscure, but it seems certain that this is the dialycal theca giving rise to $th2^1$ and $th2^2$; $th1^2$ arises very low down on $th1^1$. One notable feature is the rapid proliferation of the $th2^2$ to $th6^2$ and the strong, but diminishing, semicircular curvature of these thecae (Fig. 1c). This type of development may be referred to as the isograptid (*manubriatus*) type: it is similar to the isograptid (*gibberulus*) type in as much as $th1^1$ arises high on the sicula, and grows in contact with the sicula for much of its length, in that $th1^2$ is the dialycal theca, and the growth pattern is essentially platycalycal. It differs from the isograptid type in the simulation of a pericalycal growth pattern, and in the growth direction of the early thecae, particularly those of the secondary stipe.

Maeandrograptus

In his discussion of *Maeandrograptus schmalenseei* Bulman (1932b) noted that 'the structure of the proximal end of this genus is not quite so clear as in *Isograptus*, but seems to be essentially

of the same type . . . $th2^1$ is derived from $th1^2$ (not $th1^1$) but it arises sooner in *Maeandrograptus* than it does in *Isograptus*—before the crossing canal of $th1^2$ has passed over the sicula. This is perhaps to be regarded as the more primitive condition.'

Skevington (1965) was able to determine the proximal development of *Maeandrograptus* ? *geniculatus* from isolated examples. The bud of $th1^1$ develops on the prosicula 0.2 mm below the apex; the theca grows down along the sicula for 0.4 mm where the foramen for $th1^2$ develops. $Th1^1$ continues its growth along the sicula to the apertural region of the latter, when it curves away from the sicula. $Th1^2$ completely obscures the sicula, on the reverse side, except for its proximal and apertural extremities. There is a pronounced curvature of $th1^2$, the aperture being directed away from the sicula. $Th1^2$ is dialycal and gives rise to $th2^1$ and $th2^2$ at about the same level as in the isograptid (*hirundo*) type; $th2^1$ is, however, given off at the opposite side of the sicula from $th2^2$. Succeeding thecae bud off the preceding theca shortly after the origin of the latter.

In Victorian examples, proximal detail is never clear, but the curvature of the apertural regions of the earlier thecae away from the sicula can be seen. The *Maeandrograptus* type of development is quite similar to the isograptid type; that it is more primitive than the isograptid is open to conjecture: it is possibly a link between the isograptid (*gibberulus*) type and the manubriate type.

Oncograptus

Bulman (1936b) described and discussed his study of *Oncograptus* cf. *upsilon biangulatus* from Marathon, Texas (SM No. A 8140, A 8141). This material has been re-examined, but nothing new can be added to Bulman's conclusions. It has shown that $th1^1$ arises in the apical region of the sicula and grows down the sicula for about one half of its length, when it is separated from the sicula by the inter-position of another theca. $Th1^2$ is derived from $th1^1$ by a very broad crossing canal 'rather reminiscent of that of *Tetragraptus bigsbyi* but quite unlike that of *Isograptus gibberulus*'. From the base of the $th1^2$ the secondary stipe arises, but there is no second crossing canal. $Th1^1$ is the dialycal theca, $th2^1a$ and $th2^1b$ arising from this. $Th2^1a$ occupies the normal position on the primary stipe; $th2^1b$ is very short, and grows round sharply on the side opposite the crossing canal, taking up a position between the sicula and $th1^1$, and opening between their apertures. The proximal development of *Isograptus* and *Oncograptus* are quite dissimilar, and Bulman regarded the two genera as totally unrelated.

Skiagraptus

Whittington and Rickards (1969) found the proximal development of *Skiagraptus* to be essentially dichograptid with an incipient monopleural arrangement of the thecae. $th1^1$ is almost immediately formed and grows across the back of the sicula giving rise rapidly to $th2^2$, $th3^2$ Thecae subsequent to $th1^1$ and $th1^2$ became progressively shorter and more steeply inclined to the axis of the rhabdosome so that $th7^1$ is horizontally directed. In the early stages, when the thecae are growing downwards, each thecal tube crosses the axis of growth of the previous theca in the series. This seems to be the result of each initial bud attempting to grow at first dorsally to the previous theca and it is this which gives to the rhabdosome as a whole the incipient monopleural arrangement.

Oncograptus

Dichograptid type

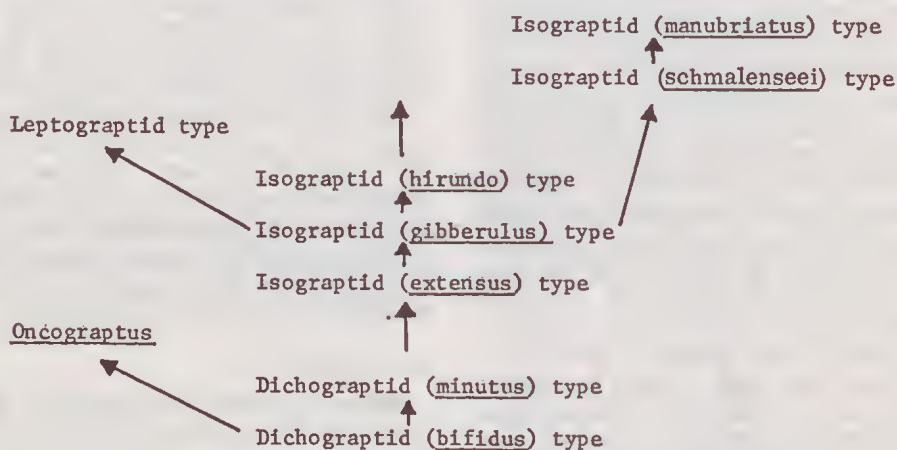
Skiagraptus

Dichograptid type

Whether, in fact, the type of proximal development is taxonomically significant at this level is debatable, and will be considered later in this paper (p. 186). The types of proximal development are, however, related: a postulated relationship is shown in Table 1.

The isograptid (*schmalenseei*) type of development differs from the isograptid (*hirundo*) type in the growth direction of the apertural region of the early formed thecae. This is accentuated in the isograptid (*manubriatus*) type, in which, also, the marked curvature of the proximal thecae is distinctive. It would appear that the development

TABLE 1



DISCUSSION

In erecting the Family Isograptidae, Harris assumed that all genera of the Family had the Isograptid (*gibberulus*) type of development. The results of the subsequent research, just summarized, show that this assumption was not valid for *Oncograptus* (and therefore presumably for *Cardiograptus* see Fig. 15j), *Pseudisograptus* or *Skiagraptus*.

The same type of proximal development, taken by Harris as one of the main taxonomic criteria at the familial level for the Isograptidae, does not in fact occur:

*Isograptus caduceus*Isograptid (*gibberulus*) type*Pseudisograptus manubriatus*

Manubriate type

*Meandrograptus*Isograptid (*schmalenseei*) type

of *Maeandrograptus* is slightly more advanced than that of *Isograptus gibberulus*, rather than being more primitive as suggested by Bulman (1932b). The budding positions of $th2^1$ and $th2^2$ on $th1^2$ in *Maeandrograptus* are similar to those shown in the isograptid (*hirundo*) type, which is a development from the *Isograptus (gibberulus)* type (Bulman, 1932b). In this paper (p. 188), stratigraphic evidence will be presented to support this idea. One important aspect which is emerging here is the close relationship of *Pseudisograptus* to *Maeandrograptus* and the intermediate position of the latter genus between the former, and *Isograptus*.

THECAL TYPES IN ISOGRAPTIDS

Although Harris had available published descriptions and plates of thecae of *Isograptus gibberulus* and *Maeandrograptus schmalenseei* preserved in a more or less uncompressed state, he

did not have the opportunity to examine such material, and all of his work was carried out on highly compressed and often poorly preserved specimens: it is remarkable that he was able to determine the amount of thecal detail which he has described. In this paper, thecal detail has been determined from the highly compressed Victorian specimens but in addition, uncompressed and isolated material from Europe and America was available for comparative purposes.

Isograptus caduceus AND RELATED SPECIES

Specimens of '*Didymograptus*' *caduceus* from the Skiddaw slates described by Elles (1898), and descriptions of Nicholson's types indicate that the thecae of *Isograptus caduceus* are simple tubes, in contact for almost their entire length. The proximal thecae are about 2 mm long and 0.7 mm wide. Distal thecae are much shorter (1.2 mm). Throughout the rhabdosome the thecae are remarkably uniform in general morpho-

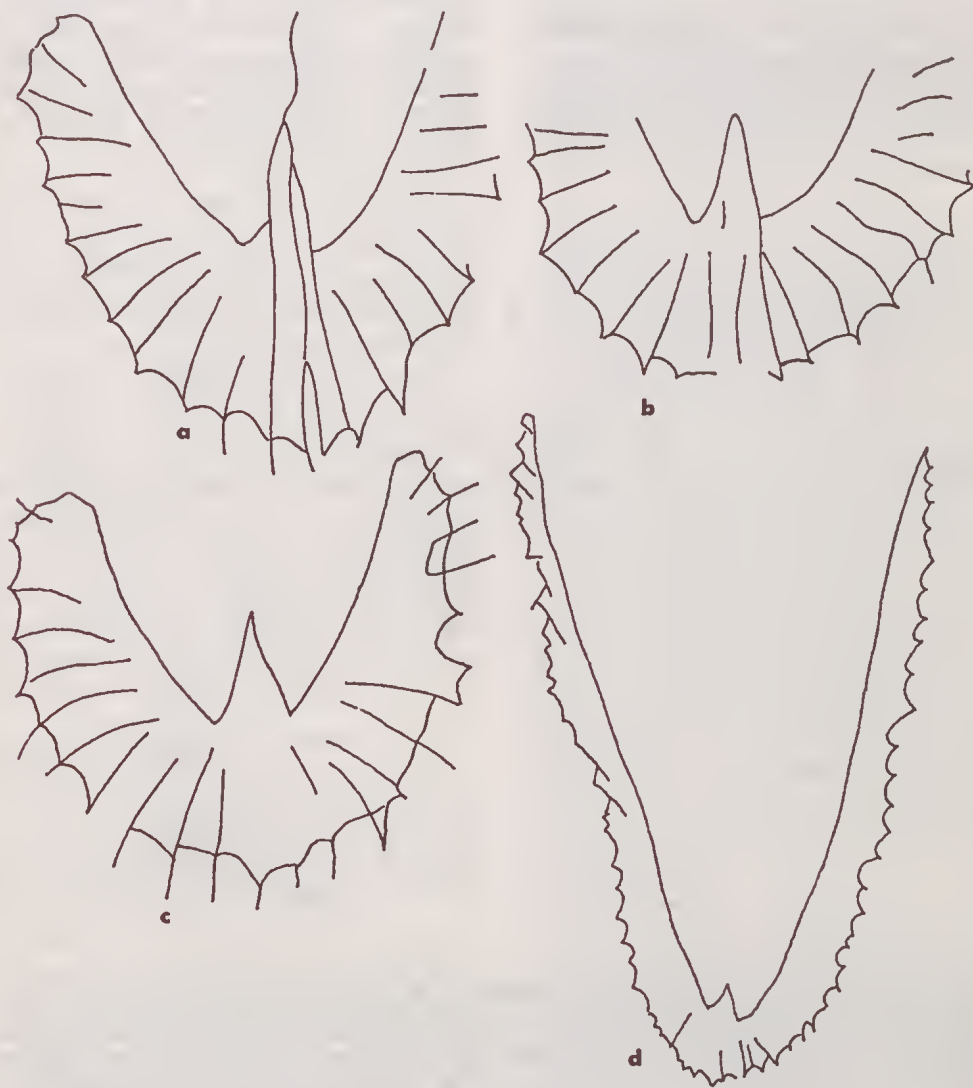


FIG. 2—*a-c* *Isograptus gibberulus* (? = *Isograptus victoriae*) Lower *Didymograptus* Shales, Killeröd, Sweden. (a) Obverse aspect SM A51315c, $\times 7.5$. (b) Reverse aspect SM A51314b, $\times 7.5$. (c) SM A51314a, $\times 7.5$. (d) '*Didymograptus*' *caduceus* SM A17779 Syntype (Elles, 1901), figured Nicholson (1875). Skiddaw Crag, Skiddaw, England, $\times 3.75$ approx.

logy and apertural characteristics. There is some slight variation in shape: all of the proximal thecae have a gentle curvature: in the distal thecae, the curvature is reduced, and some may be quite straight. Proximal thecae are pendent, the distal reclined, the change occurring gradually along the stipe. Thecal apertures are directed outwards (except for the proximal thecae, which have downward directed apertures) and are almost parallel to the stipe axis. Denticles are well developed and are almost normal to the apertural margins.

Bulman (1932b) did not give detailed descriptions of the thecae of *Isograptus gibberulus*, but his figures show that the thecae are virtually identical with those of *Isograptus caduceus*. Slightly

compressed specimens of *Isograptus gibberulus* from Killeröd, Sweden (SM Nos. A51313, A 51314, A 51315) shown here as Fig. 2 a-c have all thecae, proximal and distal, slightly curved, while a single isolated specimen (SM No. A 513152) from the same area has the first theca, th1¹, straight, but other thecae are curved.

Most of the specimens figured by Harris (1933) as varieties of *Isograptus caduceus* have been destroyed, but examples of his var. *victoriae* from the type locality, Victoria Gully, Castlemaine, indicate that the thecae of this form accord closely in most if not all respects with those of forms described as *Isograptus gibberulus*. Cooper (1971, 1972) has published a note on *I. caduceus*. His general conclusions may be supported, but the



FIG. 3.—Thecal types in Isograptids. All figures $\times 8$ approx. (a) Proximal thecae of *Isograptus victoriae* SM A6320. Victoria Gully, Castlemaine, Victoria. (b) Distal thecae in same specimen as (a). (c) Proximal thecae of *I. gibberulus* SM A51315. Killeröd, Sweden. (d) Thecae of *Pseudisograptus manubriatus* SM A60283, Wileys Quarry, Macedon, Victoria. (e) Thecae of *Maeandrograptus schmalenseei* SM A23228 Lower *Didymograptus* Shales, Killeröd, Sweden. (f) Thecae of *Maeandrograptus tau* SM A6334 Loc. Ba71, Gisborne, Victoria. (g) Thecae of *Skiagraptus gnomonicus* SM A602856 Wileys Quarry, Macedon, Victoria. (h) Thecae of *Skiagraptus* sp. After Whittington and Rickards (1969). (i) Thecae of *Oncograptus upsilon biangulatus* SM A8141 Marathon, Texas. (j) Thecae of *Oncograptus upsilon* SM A22748 Loc. Ba71 Gisborne, Victoria. (k) Thecae of *Cardiograptus morsus* SM A6323c Chinamans Ck, Muckleford, Victoria. (l) Thecae of *Cardiograptus crawfordi* SM A60284 Strathfieldsaye, Victoria. (m) Thecae of *Pseudisograptus manubriatus* SM A603142 Marathon, Texas.

recognition of the varieties of Harris as sub-species of *I. victoriae* cannot be supported.

Pseudisograptus manubriatus

Harris (1933, p. 103) commented only briefly on the thecae of this species: 'The thecae number about 8 in 10 mm, resemble those of *Isograptus caduceus* in general form, but have rather less complete overlap, and a denticle which, though pronounced, is directed outwards rather than downwards, so that the thecal apertures open upwards rather than outwards. The apertural margin is also less concave.'

Skevington (1968) did not discuss thecal characters of this species in any great detail, but he noted that the 'tuft' of thecae at the level of the aperture of the sicula reflected the deflection of apertural portions of early formed thecae away from the sicula. Bulman (1968) observed that $th1^2$ to $th6^2$ all have a strong semi-circular curvature; subsequent thecae are relatively straight. Thecal curvature in the primary stipe is considerably less. $Th1^1$ is slightly curved, and curvature of thecae in this stipe decreases so rapidly that $th6^1$ is straight. The specimen described by Bulman (SM No. A 603142) shows $th1^1$ to $th3^1$ and $th1^2$ to $th4^2$ with downward directed denticles. In later thecae, the denticles are directed outwards, and the thecal apertures open upwards. Overlap is 0.75 to 0.80. The example shows thecal characteristics which differ markedly from those of *Isograptus*, the most important of which is the incipient prothecal folding. This although not strongly marked, is sufficiently developed to distinguish the thecae from the simple tubes of *Isograptus caduceus*.

Pseudisograptus hastatus, *Pseudisograptus dumosus*, *Isograptus ovatus*

For these species only the compressed Victorian material is available for study, and, as in the case of the Victorian specimens of *Pseudisograptus manubriatus*, thecal simplicity may be apparent rather than real.

The thecae of *Pseudisograptus hastatus* are conical tubes, 10 in 10 mm, overlapping by a little more than 0.5, and with a denticle much less pronounced than in *Isograptus caduceus*. The apertural margins are slightly concave, make an angle of up to 140° with the axis of the stipe, and open upwards. In *Pseudisograptus dumosus* the thecae are simple curved tubes. Proximally, overlap is almost complete, but distally, overlap decreases. The apertural margins are straight or slightly concave, and are directed more upwards than outwards. Harris noted (1933, p. 86) that

there is a divergence from the 'typical trumpet shaped' thecae of *Isograptus caduceus*.

Isograptus ovatus has curved, expanding thecae, about 0.5 mm wide, and numbering 12 in 10 mm. Overlap is about 0.5. The apertural margins are usually deeply concave and the denticle is pronounced.

Isograptus forcipiformis

The thecae are strongly curved, and the width: length ratio (0.5) of the distal thecae is much greater than that of the proximal theca (0.20-0.24). The apertures are slightly to deeply concave, and tend to be directed outwards. Thecal overlap is almost complete. One interesting development noted in this form is an incipient monopleural arrangement of the thecae, so that there is a lateral, as well as a longitudinal overlap.

Maeandrograptus

Thecal characteristics of the Victorian species, *M. tau* and *M. aggestus* are almost impossible to determine. Harris noted for *Maeandrograptus tau* that the thecae have a low inclination, overlap is 0.3-0.5 increasing distally, and that the ventral margins are sigmoidally curved. For *Maeandrograptus aggestus* he was only able to note that 'the thecae are long tubes, circular or rectangular in cross section . . . apertures slightly concave and almost parallel to the axis of the sicula'.

Bulman (1932b) confirmed and enlarged on the earlier observations of Moberg (1892) and Törnquist (1901). The first two thecae on each stipe are shorter than the remainder, and overlap is considerably less. Later thecae increase greatly in length with an increase in overlap. The early thecae are flexed, but distal thecae, up to 7 mm long and 0.25 mm wide are almost straight. All of the thecae have a prominent denticle. Skevington (1965) drew attention to the prothecal folding, a feature absent from the thecae of *Isograptus*. At their origins, the interthecal septa bend into the prothecal folds.

Bulman (1969) commented on Skevington's work, noting that *Maeandrograptus ? geniculatus* has thecae closely resembling those of *Isograptus* in all respects other than the prothecal folds 'of a simple type'. Bulman appears to be hesitant to regard *Maeandrograptus* as being other than closely related to *Isograptus*, in spite of the differing thecac.

Oncograptus AND *Cardiograptus*

It is clear from uncompressed material (SM No. A 8140, A 8141 Bulman 1936b) that in the proximal region of the rhabdosome of *Oncograptus*

there is a progressive deflection of thecal apertures away from the sicula. The apertural margins appear to be straight (although this is not always clear) and are directed outwards. Denticles are prominent and may be directed downwards or outwards. The thecae are relatively long, narrow tubes, with a strong sigmoidal curvature. Overlap is 0.8 to 0.9.

With only compressed specimens available, it is difficult to determine the thecal characteristics of *Cardiograptus*. They appear to be relatively simple tubes with a slight curvature. Apertural margins are straight to slightly concave, are directed downwards in the proximal thecae, and outwards in the distal thecae. The proximal thecae are strongly denticulate, but the distal thecae have less prominent denticles. Throughout, denticles are directed downwards.

Skiagraptus

In the type specimen of the Victorian *Skiagraptus gnomonicus* the proximal thecae grow along the sicula with their apertures opening downwards. The later thecae, apparently horizontal, have apertures directed downwards. Denticles are prominent. Whittington and Pickard (1969) described the thecae of *Skiagraptus* as simple, short and straight with a short dorsal process; the length of the distal thecae is much less than that of the proximal. Thecal apertures are rectangular.

ISOGRAPTID-LIKE DIDYMOGRAPTIDS: *Didymograptus eocaduceus* AND *D. hemicyclus*

These two species of *Didymograptus* have rhabdosomes which closely resemble *Isograptus*. In *D. eocaduceus* thecae are simple, slightly curved tubes, with overlap 0.50 to 0.65. The denticle is pronounced, and is directed outwards or slightly downwards. Apertural margins are concave and are directed upwards, making an angle of 100° to 125° with the stipe axis. In *D. hemicyclus* the thecae are long conical tubes, with overlap 0.30. The ventral and apertural margins are slightly curved. The denticle, often quite prominent, is directed outwards, or sometimes downwards.

DISCUSSION

One of the diagnostic characteristics of the Isograptidae defined by Harris was the simplicity ('*Didymograptus* type') of the thecae. *Isograptus caduceus* and its closely related species (the varieties of Harris), *I. forcipiformis* and *Oncograptus*, *Cardiograptus* and *Skiagraptus* all have such simple thecae. In *Maeandrograptus* and *Pseudisograptus*, however, the thecae are more complex types with protheal, and in the proximal thecae

of *Maeandrograptus schmalensei* at least, longitudinal lateral wall folding. Moreover, the thecae lose the simplicity of those of the true *Isograptus*.

Apertural characteristics are surprisingly constant, although there is evidence that the apertures in *Maeandrograptus* and *Pseudisograptus* are more complex than in *Isograptus*. The suggestion of Harris that there is a progression, and then a regression in the apertural form of thecae of *I. caduceus* and closely related species is confirmed. Apart from this, no definite trends have been discerned.

RHABDOSOMAL CHARACTERISTICS OF THE ISOGRAPTIDS

The most obvious rhabdosomal feature of the isograptids is the reclined to scandent attitude of the stipes. All genera consist of two stipes: *Oncograptus* is proximally biserial, distally dividing into two uniserial stipes, while *Cardiograptus* and *Skiagraptus* are dipleural, and scandent throughout. The tendency towards a scandent growth direction and conerescence in the genera *Oncograptus*, *Cardiograptus*, and *Skiagraptus* was seen by Harris as one of the major evolutionary trends of the isograptids. There was some stratigraphic evidence to support this hypothesis: at least some of the evidence is not always convincing.

In this section, the rhabdosomal characteristics of the isograptids will be considered with special reference to size and spacing of thecae, angle of stipe divergence, and form of the proximal part of the rhabdosome, all of which have some taxonomic significance. The rhabdosomal (and thecal) characteristics are summarized in Table 2.

Isograptus gibberulus AND CLOSELY RELATED SPECIES

In the specimens of *Isograptus gibberulus* described by Bulman (1932b) the stipes are 2 cm long and decrease in width from 2.5 mm at their origin to 1 mm distally. Thecae number 10 to 16 in 10 mm. Proximally, the angle of divergence of the stipes is 270° but distally it is 320° to 330°. Proximally, the thecae grow almost parallel to the sicula.

Examples of '*Didymograptus*' *gibberulus* described by Elles (1898) from the Skiddaw slates have stipes 2 mm wide proximally, tapering to 1.0 to 1.25 mm distally. Angle of stipe divergence is 335° to 340°, and thecae number 16 in 10 mm. Elles distinguished three groups of varieties of *I. caduceus*, mainly on the basis of angle of divergence:

- (i) dorsal walls of stipes continuously curved so that the distal extremities point towards each other;

Table 2

Thecal Characteristics												Rhabdosomal Characteristics										Remarks : Including direction of thecal apertures	
Species	Shape Proximal	Shape Distal	Length mm		Width mm		Growth Direction		Aperture	Direction of Denticle	Overlap %	No. of Stipes	Stipe Length cm	Stipe Width mm		Stipe shape	Divergence	Sicula Length mm	Thecae in 10 mm	Initial Growth			
Isograptus victoriae	Straight	Sigmoidal	2.0	1.2-1.5	0.6	0.6	Pendent	Scandent	Concave	Outwards	90	2	1.0+	2.5	2.0	Slight curvature	P250° D305-310°	4.5-5.0	11-12	'gibberulus'	Thecal apertures directed outwards. space between sicula and thl ¹ .		
Isograptus gibberulus	Straight	Sigmoidal	2.0	1.3	0.7	0.5	Pendent	Scandent	Concave	Outwards	90	2	0.5	2.0	1.0	Curved	P180° D290-300°	4.5-5.0	13	'gibberulus'	space between sicula and thl ¹ .		
Isograptus primulus	Straight	Straight	1.0	0.4	0.5		Pendent	Reclined	Slight Curvature	Downwards	80-90	2	0.5	2.0	1.0	Curved	P180° D290-300°	2.5	10-12	'gibberulus'	Stipes narrow rapidly.		
Isograptus lunatus	Straight	Straight	1.0	0.6	1.0	0.6	Pendent	Reclined-Scandent	Concave	Downwards and Outwards	100	2	1.0	1.5+	1.0+	Straight	295-310°	3.0	11-14	'gibberulus'	Thecal apertures directed outwards or upwards		
Isograptus maximus	Sl. curved	? Straight	2.5-4.0		0.7-0.8		Pendent	Scandent	Concave	Downwards	90+	2	1.5-2.0	2.0	2.0	Straight to Sl. curved	300-310°	5.5-6.0	10-11	'gibberulus'	Thecal apertures directed outwards.		
Isograptus maximodivergens	Strongly curved	Curved	2.5-3.0	2.5-3.0	0.4	0.3 ⁺	Pendent	Reclined	Concave	Downwards and Outwards	90+	2	2.5-3.0	2.5	up to 4.0	Straight to Sl. curved	315-325°	2.5+	8-9	'gibberulus'	Very large specimens known. Thecal apertures directed outwards.		
Isograptus divergens	Curved	Curved	4.0	4.5	2.0	2.5	Pendent	Reclined	Concave	Downwards	80-90	2	4.0	2.0	2.5	Straight-curved	330-335°	3.0	10-11	'gibberulus'	Thecal apertures directed outwards.		
Isograptus imitatus	Straight-curved	Straight	1.5+	1.0 ⁺	0.5 ⁺	0.5 ⁺	Pendent	Reclined	Straight	Downwards	80-100	2	1.5	3.0	2.0-2.2	Straight	325-340°	2.5-5.0	8-10	'gibberulus'	Thecal curvature increases distally; apertures directed outwards.		
Isograptus velatus	Straight-curved	Straight	1.5-2.0	0.9-1.1	0.6	0.5	Pendent	Reclined	Straight	Downwards	60	2	0.5	1.5-2.0	1.0	Slightly curved	330-340°	3.0	9-10	? 'gibberulus'	Thecal apertures directed outwards for all thecae.		
Isograptus tenuis	Straight	Straight	0.7	0.7	0.4	0.4	Pendent-Horizontal	Reclined	Straight	Outwards	30	2	0.6	0.6	0.6	Curved	300-305°	1.3+	12-14	? 'gibberulus'	Stipes very slender. Thecal apertures directed outwards.		
Isograptus harrisi	Curved	Slightly curved	1.7	1.25	0.5	0.4-0.5	Pendent	Reclined	Concave	Outwards	85-100	2	0.3-0.5	1.8-2.0	0.8-0.9	Curved	P180°D330°	3.6	13-15	'gibberulus'			
Pseudisograptus manubriatus	Curved	Straight	2.0	4.0	0.7-1.0	1.0-	Pendent-Curved	Reclined	Concave	Outwards Upwards	60	2	1.0+	2.8 ⁺	3.0 ⁺	Straight	130-140°P 300°D	6-8	10	'manubriatus'	Initial growth modified Isograptid : 'platycalycal'. Thecal apertures directed upwards.		
Pseudisograptus hastatus	Straight	Straight	1.0-1.5	1.0	0.4-0.5	0.4-0.5	Pendent-Curved	Reclined	Slightly Concave	Outwards	50-60	2	1.0	0.7	0.6	Tapering	330°	5.0-6.0	10-12	'manubriatus'	Thecal apertures directed upward except in sicular region.		
Pseudisograptus dumosus	Curved	Curved	1.5	1.4 ⁺	0.4	0.45	Pendent-Curved	Reclined	Concave	Outwards	0.95P 0.70D	2	0.4 ⁺	1.0	0.7	Curved	330-360°	3.5+	8-9	'manubriatus'	Thecal apertures directed upward.		
Isograptus ovatus	Curved	Curved	1.5	1.5	0.5	0.5	Pendent	Reclined	Concave	Outwards and Downwards	50	2	1.0	1.0	1.0	Curved	360°+ Dist.	3.0 ⁺	12	? 'manubriatus'	Thecal apertures directed outwards.		
Isograptus forcipiformis	Curved	Curved	1.2	1.0	0.5	0.4	Pendent	Reclined-Scandent	Concave	Downwards	100 -	2	0.7	4.0	1.0	Straight	360°	3.5-4.0	9-11	'gibberulus'	Thecal apertures directed outwards and upwards (distally).		
Isograptus pertensus	Straight	Straight	4.0	1.5	0.7	0.7	Pendent	Scandent	Concave	Downwards-Outwards	95	2	6-8	3.0	1.5	Straight	340°	7.5	6-7	? 'gibberulus'	Thecal apertures directed outwards.		
Oncograptus upsilon	Curved	Sigmoidal	5.0	4.0	1.0	0.8	Pendent	Scandent	Concave	Downwards	90-100	Biserial Uniserial (2)				Straight	330°		12-13	Dichograptid) Length of uniserial stipes varies widely. Thecal apertures)) directed outwards and upwards.		
Oncograptus upsilon biangulatus	Curved	Sigmoidal	5.0	4.0	1.0	0.8	Pendent	Scandent	Concave	Downwards	90-100					Straight-curved	335-340°		12-13	Dichograptid			
Cardiograptus morsus	Curved	Sigmoidal	3.0	6.0	?	0.9	Pendent	Reclined	Concave	Outwards and Downwards	95-100	Biserial							10	? Dichograptid	Thecal apertures directed outwards. Rhabdosome up to 2.0 cm. long.		
Cardiograptus crawfordi	Curved	Slightly curved	2.0	2.6	0.6	0.5	Pendent	Scandent	Concave	Downwards and Outwards	100								11-13	? Dichograptid	Thecal apertures directed outward.		
Skiagraptus gnomonicus	Curved, short	Curved	1.0	1.5	0.5	0.5	Pendent	Scandent	Straight Concave	Downwards and Outwards		Biserial							12-13	Dichograptid			
Maeandrograptus tau	Sigmoidal	Sigmoidal	1.5		0.4			Horizontal	Horizontal	Concave	Downwards		2	0.5	1.0	0.8	Straight	180°+	2.5-5.5	9	Maeandrograptid	Modified Isograptid initial development.	
Maeandrograptus aggestus	Sigmoidal	Straight?	1.2		0.3			Horizontal	Horizontal	Straight	Downwards	2				Straight	180°	2.5		Maeandrograptid	Modified Isograptid initial growth.		

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- (ii) dorsal walls straight, so that the stipes are parallel;
- (iii) dorsal walls straight; distal extremities directed away from each other.

Isograptus victoriae (the var. *victoriae* of Harris) in Victoria has rhabdosomal characteristics which correspond closely with those of *I. gibberulus*. Distally the stipes diverge at 330° proximally; the angle of divergence is 260° to 290°. The form was described by Harris as 'horse-shoe shaped'. Stipes are 1.5 to 2.0 mm long, and narrow from a width of 2 mm proximally to 1.0 to 1.2 mm distally. Dorsal walls of the stipes have a slight curvature. Thecae number 10 to 15 in 10 mm.

Isograptus primulus, the first of the isograptids to appear in Victoria, has a small rhabdosome, with stipes consisting generally of only 2 or 3 thecae. The stipes are wide in the sicular region, but narrow rapidly. *I. lunatus* has the external form of *I. caduceus* except that the dorsal stipe walls are more strongly curved in the style of Elles' variety (i). The stipes are narrow, and have a uniform width. The dorsal stipe walls of *I. maximus* may be straight or slightly curved with an angle of divergence equal to, or slightly more than that of *I. caduceus*. The stipes maintain a uniform width throughout, but the dimensions may be as much as twice those of *I. caduceus*. An increase in the angle of divergence, and a narrowing of the stipes at the point of flexure characterize *I. maximo-divergens*. Stipes in this species may be 5 cm long and 5 mm wide. *I. divergens* is marked by the thinness of the stipes and a decrease in robustness of the rhabdosome.

Harris regarded *I. pertensus* as a variety of *I. caduceus* closely related to *I. divergens*, but Beavis and Beavis (1968) described it as a distinct species. In *I. pertensus* the stipes may reach a length of 10 cm. Angle of divergence is proximally 340°, and gradually the stipes become parallel. The sicular region is spinose and distally there are only 7 thecae in 10 mm. The var. *horrida* of Harris is identical with *I. pertensus* in every respect except size.

The stipes of *I. forcipiformis* are parallel to each other and are up to 2 cm long. Initially over 2 mm wide, the stipes taper until they are 1 mm or less in width. The narrow space between the dorsal walls of the two stipes is characteristic. *I. imitatus* varies considerably in size, but is otherwise close to *I. lunatus*. *I. tenuis* is an attenuated 'horse-shoe' shaped form with a thin periderm, while *I. velatus* has some characteristics of the manubriate isograptids. *I. ovatus*, also closely related to the manubriate species, has stipes of uniform width, about 1 mm, with the dorsal margins

strongly curved. The stipes may reach a length of 1 cm. Angle of divergence varies, and the distal extremities of the stipes may be directed towards each other.

THE 'MANUBRIATE' SPECIES: *Pseudisograptus manubriatus*, *P. hastatus* AND *P. dumosus*

These forms have, apparently, a thickened sicular region. Hall (1914) ascribed this to a wide sicula; Harris, however, regarded it, correctly, as being due to the growth pattern of the first few thecae. In the species *P. manubriatus* the stipes vary in width from 2 to 3 mm and diverge initially at 300°. The thecae number 10 in 10 mm. Skevington (1968) examined this form in detail, and found an initial angle of divergence of 30°, later increasing to 130°-140° and ultimately to 300°. Beyond the sicular region, the stipes maintain a more or less uniform width.

P. hastatus has a small rhabdosome with stipes about 1 cm long, diverging ultimately at 330°. The stipes taper slightly. Thecae number 10 to 12 in 10 mm. The rhabdosome of *P. dumosus* is small, usually less than 5 mm in length. The dorsal walls of the stipes are strongly curved, but distally the dorsal walls are straight and the stipes are parallel to each other.

Oncograptus AND *Cardiograptus*

In *Oncograptus* the proximal region of the rhabdosome is biserial, but distally there is a bifurcation into two uniserial stipes. *O. upsilon* is 10 to 14 mm wide at the bifurcation, and the angle of divergence of the uniserial stipes is 320° to 330°. *O. upsilon biangulatus* is less than 10 mm wide at the bifurcation, with the uniserial stipes inclined at 330° to 340°. The uniserial stipes of *O. upsilon* are 5 mm wide; in *O. upsilon biangulatus* the width is invariably less than 5 mm.

Harris postulated (1933, p. 96) that 'the failure of *Oncograptus* to develop its uniserial stipes would result in a wholly biserial form. *Cardiograptus* is such a form'. In both known Victorian species of *Cardiograptus* the rhabdosome is 'heart shaped', but more so in *C. crawfordi* than in *C. morsus*. Two quite distinct forms of *C. morsus* occur: a broad form, and a narrow, but within each, the width varies between wide limits.

Maeandrograptus

The rhabdosome is small, each stipe being usually not more than 1 cm long. The sicula is long and slender, there is a slight tendency for a concentration of thecal origins in the sicular region. The distal thecae are excessively long, and have a very low inclination. The dorsal stipe walls are

undulating, due to prothecal folding. Angle of divergence varies from 180° to 270°.

Skiagraptus

The rhabdosome of this genus is small: usually about 8 mm long, and 2 mm, or slightly less, wide. The thecal arrangement is dipleurial, with an incipient monopleurial development and the stipes are scandent, giving a biserial form. In the Victorian *S. gnomonicus* each stipe normally consists of about 8 thecae.

A REVISED CLASSIFICATION OF THE ISOGRAPTIDS

The formal diagnosis of the family Isograptidae Harris (1933, p. 100-101) reads:

Biserial, initially biserial, or uniserial forms with stipes diverging at 180° or more, the proximal thecae growing at first entirely downwards and either opening in this direction or turning outwards, later thecae tending to become scandent. Thecae of the general type of *Didymograptus*.

Although he did not categorically assert that the isograptid type of development was the main basis for the Family, Harris implied this a number of times; he regarded also the direction of growth of the stipes as of major taxonomic importance. In classifying the isograptids the question of similar, or differing, thecal and rhabdosomal morphology is an important one: the relative significance of these at the several taxonomic levels is not always clear. It is, however, generally agreed that thecal characteristics are the most important in familial separation. On this basis, since, with the exception of *Maeandrograptus* and *Pseudisograptus* the thecae are didymograptid, the genus *Isograptus* must be regarded as a dichograptid, and the family defined by Harris reduced in status to a sub-familial level. At this level, it would seem that such criteria as angle of divergence and proximal development are significant, so that it is proposed to include here in the sub-family Isograptinae those species with a reclined growth direction and with the proximal development of the isograptid (*gibberulus*) type.

The sub-family Isograptinae (Harris) includes the single genus *Isograptus*. *Oncograptus* and *Cardiograptus* are included in the sub-family Cardiograptinae (Mu and Zhan). *Maeandrograptus* and *Pseudisograptus* have thecal characteristics of the sinograptids, and if thecal characteristics are to be the main criterion in familial distinction, then full familial status must be accorded to this group and not merely a sub-familial status as suggested by Bulman (1963). The inclusion of

Maeandrograptus in the Family Sinograptidae Mu has been challenged by Bulman (1969). He states (p. 14):

TABLE 3
CLASSIFICATION OF THE VICTORIAN ISOGRAPTIDS

Order	GRAPTOLOIDEA Lapworth 1875
Sub-order	DIDYMOGRAPTINA Lapworth 1880 (amend)
Super-family	DICHOGRAPTACEA Lapworth 1873
Family	DICHOGRAPTIDAE Lapworth 1873
Genus	<i>Didymograptus</i> McCoy 1851 <i>Didymograptus eocaduceus</i> Harris <i>Didymograptus hemicyclus</i> Harris
Genus	<i>Skiagraptus</i> Harris 1933 <i>Skiagraptus gnomonicus</i> (Harris and Keble)
Sub-family	ISOGRAPTINAE (Harris) 1933
Genus	<i>Isograptus</i> Moberg 1892 <i>Isograptus victoriae</i> Harris <i>Isograptus primulus</i> Harris <i>Isograptus lunatus</i> Harris <i>Isograptus maxinus</i> Harris <i>Isograptus maximodivergens</i> Harris <i>Isograptus divergens</i> Harris <i>Isograptus pertensus</i> Harris <i>Isograptus unitatus</i> Harris <i>Isograptus velatus</i> Harris <i>Isograptus tenuis</i> Harris <i>Isograptus ovatus</i> T. S. Hall <i>Isograptus harrisi</i> n. sp. <i>Isograptus forcipiformis</i> Ruedemann
Sub-family	CARDIOGRAPTINAE (Mu and Zhan) 1966
Genus	<i>Oncograptus</i> T. S. Hall 1914 <i>Oncograptus upsilon</i> T. S. Hall <i>Oncograptus upsilon biangulatus</i> Harris and Keble
Genus	<i>Cardiograptus</i> Harris and Keble 1916 <i>Cardiograptus morsus</i> Harris and Keble <i>Cardiograptus crawfordi</i> Harris
Family	SINOGRAPTIDAE Mu 1957
Genus	<i>Pseudisograptus</i> Beavis 1972 <i>Pseudisograptus manubriatus</i> (T. S. Hall) <i>Pseudisograptus hastatus</i> (Harris) <i>Pseudisograptus dumosus</i> (Harris)
Genus	<i>Maeandrograptus</i> Moberg 1892 <i>Maeandrograptus aggestus</i> Harris <i>Maeandrograptus tau</i> Harris

extend its scope considerably by introducing new values.

Although Bulman argues convincingly, it is considered that *Maeandrograptus* should be referred, at least tentatively, to the Family Sinograptidae Mu. The reference of *Pseudisograptus* to this

Species	Zone											UO
	Ch1	Ch2	Ca1	Ca2	Ca3	Ya1	Ya2	Da1	Da2	Da3	Da4	
<i>Isograptus primulus</i>		-----										
<i>I. lunatus</i>		-----										
<i>I. victoriae</i>				-----								
<i>I. maximus</i>					-----							
<i>I. maximodivergens</i>						-----						
<i>I. divergens</i>						-----						
<i>I. imitatus</i>						-----						
<i>I. tenuis</i>												-----
<i>I. pertensus</i>						-----						
<i>I. forcipiformis</i>						-----						
<i>I. ovatus</i>												
<i>I. harrisi</i>												
<i>Pseudisograptus manubriatus</i>						-----						
<i>P. hastatus</i>						-----						
<i>P. dumosus</i>						-----						
<i>Oncograptus upsilon</i>						-----						
<i>O. upsilon biangulatus</i>							-----					
<i>Cardiograptus morsus</i>							-----					
<i>C. crawfordi</i>												
<i>Maeandrograptus aggestus</i>						-----						
<i>M. tau</i>						-----						
<i>Skiagraptus gnomicus</i>						-----						

Family is even more doubtful, but there is no question that while the thecal characteristics are not maeandrograptid (Beaves, 1972) they are certainly not dichograptid. On the evidence at present available, there seems to be no basis for regarding *Oncograptus* and *Cardiograptus* as sino-graptids as suggested by Skevington (1968).

Skiagraptus has thecae of the general dichograptid type (Whittington and Rickards, 1969) although showing some departures from the simpler dichograptid thecae. The proximal development is of a modified dichograptid type, and on these grounds, this genus is referred to the Family Dichograptidae Lapworth.

In his paper, Harris (1933) discussed and figured a number of forms which he referred to as 'varieties' of *Isograptus caduceus*. On the basis of such criteria as thecal apertures, angle of divergence, and rhabdosomal morphology in general, these varieties are to be regarded as separate and distinct species of *Isograptus* and not as subspecies of *I. victoriae*. *Isograptus caduceus* var. *victoriae* was stated to be the 'forma typica'. After the examination of a large number of examples of this form, and after comparison with European examples of *Isograptus gibberulus*, we are convinced these are conspecific; however, the Victorian form is here tentatively referred to as *Isograptus victoriae*. This form is certainly distinct from the form described by Cooper (1971, 1973) as *I. caduceus caduceus*.

The isograptid, and isograptid-like forms in Victoria comprise 25 species of 7 genera. In terms used by Australian geologists, *Didymograptus eocaduceus* and *D. hemicyclus*, are not part of the 'Isograptid Fauna'. The Isograptid Fauna ranges from the Chewtonian to the Darriwilian (from the *D. nitidus* subzone to the *D. hirundo*, or *D. bifidus* Zones, of Great Britain). *Didymograptus eocaduceus* and *D. hemicyclus* are Bendigoian species.

STRATIGRAPHIC ASPECTS OF THE ISOGRAPTIDS IN VICTORIA

For stratigraphic purposes it is highly desirable to retain the term 'Isograptid Fauna' for the genera *Isograptus*, *Pseudisograptus*, *Skiagraptus*, *Maeandrograptus*, *Cardiograptus* and *Oncograptus* as together they form a distinct bio-unit of great stratigraphic importance in Victoria. The stratigraphic range of each species is shown in Table 4. The stratigraphic value of the fauna is clearly demonstrated by the Table. In particular, the restricted range of many of the species is emphasized. The rapid development of the isograptids in the Castlemanian is also illustrated,

and stratigraphic support for the contention of Harris that *I. primulus* → *I. lunatus* → *I. victoriae* → *I. maximus* → *I. maximodivergens* → *I. divergens* is obvious.

The isograptids appear first in the Chewtonian Ch2 Zone of *Didymograptus protobifidus* with *I. primulus* and, towards the top of the zone, *I. lunatus* enters. *I. primulus* is relatively short lived, but *I. lunatus* persists to the top of Ya1, although it is not common above Ca2. The isograptids have their maximum development in the Castlemanian and Yapeenian when they dominate the fauna, with a few didymograptids, phyllograptids, and rare tetrograptids occurring sporadically.

The Yapeenian is marked by the incoming of completely new forms: *Oncograptus* and *Cardiograptus*, and the appearance of *Pseudisograptus*. At the top of the Yapeenian, many of the isograptids become extinct, only a few species surviving into the Darriwilian, with only three new species appearing in the Darriwilian and one in the Upper Ordovician. The species *I. tenuis* is the only isograptid so far recorded from the Upper Ordovician, and it is known from only one locality. It is clear that the isograptids become totally extinct early in the Upper Ordovician.

With increasing knowledge of the Isograptid Fauna, a finer subdivision of the Castlemanian-Yapeenian may be possible. Ripper (1932) has suggested a subzone of *O. upsilon biangulatus*, while Harris and Thomas (1939) suggested the division of the Ya2 Zone into two subzones. Experience has shown that this suggestion is quite practicable in the field:

Subzone Ya2b

Oncograptus upsilon biangulatus
Cardiograptus morsus

Subzone Ya2a

Oncograptus upsilon
Cardiograptus morsus

DEVELOPMENT AND EVOLUTION OF THE ISOGRAPTID FAUNA

The evolution of the Isograptid Fauna is a problem, and the various workers involved have failed to agree on its solution. Harris used both palaeontological and stratigraphic data, and while there has been some quite strong criticism of some of his ideas, in particular those relating to the 'conrescent tendency' (e.g. Bulman 1936b, Skevington, 1968), as Thomas (1960) pointed out, 'Harris' general picture is logical, and because of its strong stratigraphic support it should not be dismissed too lightly'.

Isograptids appear quite suddenly in Victoria

with the relatively simple *I. primulus*. Although reclined Isograptus-like species occur in the Bendigonian (*Didymograptus eocaduceus* and *D. hemicyclus*) there is no apparent connection between these and the isograptids.

As already noted, no doubt exists on either palaeontological or stratigraphical evidence that the isograptids developed in the sequence: *I. primulus* → *I. lunatus* → *I. victoriae* → *I. maximus* → *I. maximodivergens* → *I. divergens*. Harris claimed that this sequence showed four well marked trends:

- (i) increase in size of the rhabdosome with a more open spacing of thecae;
- (ii) increase in angle of divergence;
- (iii) increasing downward-direction of denticles;
- (iv) increasing thecal overlap.

Data relating to some of these trends are shown on Table 5.

Examination of the data, based on measurements of at least 30 specimens of each species, suggests that, even allowing for variations to be expected in biological systems, some of the 'trends' postulated by Harris are apparent rather than real. Thus, while there is no question regarding increase in size of the rhabdosome (expressed here in terms of stipe-length), or of increasing angle of divergence, the so called trends in thecal overlap and thecal spacing cannot be substantiated. In spite of this, there seems no doubt that these species represent a true evolutionary sequence, the palaeontological evidence in favour of the sequence being strongly supported by the stratigraphic evidence.

The main difficulties arise in some of the other postulates of Harris regarding the development of the isograptids:

- (i) the 'manubriate tendency' with *I. maximus* giving rise to *P. manubriatus* and allied forms;

- (ii) the 'conrescent tendency' along two lines from *I. divergens*:

- (a) giving rise to *Oncograptus* and thence *Cardiograptus*
- (b) giving rise to *I. tenuis*, *I. forcipiformis* and *Skiagraptus*.

These postulates have been criticized on palaeontological grounds. In fact, some of the stratigraphic data is also in error, and conclusions drawn therefrom are invalid. The most criticized postulate is that which derives *Oncograptus* (and *Cardiograptus*), from *Isograptus*. Bulman (1936b) expressed the view that *Oncograptus* was related to a tetragraptid. He showed quite convincingly that *Oncograptus* had no clear relationship with *Isograptus* and that it was 'derived from a tetragraptid in which the mode of development has not even progressed to the *minutus* stage of the dichograptid type It hardly seems probable that a proximal end with the structure of *Oncograptus* could progress further towards the diplograptid type of development, and hence that *Cardiograptus* . . . could be the ancestor of any "normal" diplograptid'.

Bouček and Pribyl (1951) considered *Oncograptus* and *Cardiograptus* to have developed from *Isograptus*, which they derived from a tetragraptid ancestor. Thomas (1960) maintained (and he stated that Harris also held this view) that the isograptids are one of the links connecting the dichograptids with the diplograptids. *Isograptus* marks the stage at which th1² is dicalycal, and some of the later forms may have 3 crossing canals (although Thomas admitted this was not proved) and therefore follow the leptograptid type of development. He claimed two lines of development that became apparent:

- (i) a concentration of crossing canals on the apical part of the sicula (the 'manubriate' species);

TABLE 5

Species	<i>primulus</i>	<i>lunatus</i>	<i>victoriae</i>	<i>maximodivergens</i>	<i>divergens</i>
Thecae in 10 mm	10-12	11-14	11-12	8-9	10-11
Thecal overlap	0.80-0.90	1.00	0.90	0.95	0.90
Divergence	290°-300°	295°-310°	305°-310°	315°-325°	300°-310°
Length of stipe	5 mm.	10 mm.	10 mm.	25-30 mm.	15-20 mm.

- (ii) a concentration of crossing canals on the apertural part of the sicula (e.g. *Maeandrograptus*).

Thomas suggested that the former is one line of ascent of scandent forms, and the latter to the leptograptids. *Oncograptus* and *Cardiograptus* are on a side branch which, perhaps by retrogression soon become extinct. There seems to be little or no evidence to support this hypothesis.

Mu and Zhan (1966) stated that *Cardiograptus* is derived from *Oncograptus* (a point which has never been disputed) and that the Chinese material supports Harris' ideas on the origin of *Oncograptus*. Their statement, however, is of little value since they present no evidence of any kind.

The origins of *Skiagraptus* are unknown: it is a dichograptid, and its ancestry must be sought in more primitive dichograptids. It certainly did not originate from *Isograptus forcipiformis*, although having an incipient monopleural arrangement of thecae, and it lacks an isograptid type of proximal development. *I. forcipiformis* appears first high in the Ca3 zone, after *Skiagraptus* which appears first in the Ca2.

The palaeontological evidence supports the idea that *Pseudisograptus* evolved from *Maeandrograptus*: thecal types are similar, and there is an advance in the type of proximal development. There is probably a link between the isograptid (*gibberulus*) type of *I. caduceus* and the isograptid (*schmalensei*) type of *Maeandrograptus* with the isograptid (*hirundo*) type development, but this has not been found yet in Victoria.

The postulated evolutionary relationships of the Isograptid Fauna in Victoria are shown in Table 6. In summary, it may be stated, that, while *Oncograptus* is almost certainly derived from a tetragraptid ancestor, there is no satisfactory evidence pointing to the ancestry of *Skiagraptus*.

SYSTEMATIC PALAEONTOLOGY

All of the forms included by Harris in his Family Isograptidae are described and figured in this section of the paper, together with several superficially similar but unrelated species. It would have been desirable in preparing the diagnoses of the species to have referred to the holotypes: where possible this has been done, but since most of Harris' figured specimens were accidentally destroyed by fire, in the majority of cases lectotypes have been selected. These, with one or two exceptions are lodged in the Sedgwick Museum, Cambridge. In every case, descriptions have been based solely on Victorian material: relevant comparative notes on American, European and British examples have, however, been included.

Order GRAPTOLOIDEA Lapworth 1875
Sub-order DIDYMOGRAPTINA Lapworth 1880
(emend)

Super-family DICHOGAPTACEA Lapworth 1873
Family DICHOGAPTIDAE 1873

Genus *Didymograptus* McCoy 1851

Didymograptus eocaduceus Harris 1933

(Fig. 4a, b)

1933 *Didymograptus eocaduceus* Harris

MATERIAL: Lectotype NV No. 13800. Figured Harris 1933 Plate VI Figure 8A, Fig. 4a this paper. Other material examined: 33 specimens in GS collection. Preserved as limonite film on fawn slate.

HORIZON AND LOCALITY: Bendigonian Zone Bel-2. Known only from Allot. 16, Parish of Campbelltown, Victoria.

DIAGNOSIS: *Didymograptus* with stipes diverging initially at 180°, then becoming parallel, or convergent distally. Thecae simple cylindrical tubes, with concave apertural margins.

DESCRIPTION: The sicula is 1.5 mm long and about 0.5 mm wide at the aperture. The stipes vary in length from 0.5 cm to 1 cm, although one specimen with stipes 1.4 cm long was noted. Proximally the stipes are 0.8 mm wide, and narrow to 0.6 mm at the second or third thecae. They then widen to 1.0 mm and maintain this width for the remainder of their length. Initially the angle of divergence is 180° but at about the third thecae on each stipe, divergence increases so that the stipes are parallel, or in some cases converge.

Thecae are simple straight or curved tubes, 2 mm long and 1 mm wide. The apertural margins are usually straight, and they may be slightly concave; they are directed upwards, and make an angle of 95° to 135° with the axis of the stipe. Thecal spacing is constant with 11-12 thecae in 10 mm. Overlap is 0.5.

REMARKS: Superficially this form resembles *Isograptus victoricae*. However, proximal development is clearly a simple dichograptid type. The thecae have much less overlap, the apertural margins are straighter, and are differently directed. The denticle, though pronounced, is less prominent than in *Isograptus*. This form is unrelated to *Isograptus*: it occurs in an isolated fauna notable for the number of species unique to it. It is probable that it developed from a reclined tetragraptid ancestor, by a failure of dichotomy.

Didymograptus hemicyclus Harris 1933

(Fig. 4c, d)

1933 *Didymograptus hemicyclus* n. sp. Harris

MATERIAL: Lectotype NV No. 13797. Figured Harris (1933) Plate VI Figure 4. Fig. 4c of this paper. Other material examined: 21 specimens GS collection. All material limonite films on fawn slate.

HORIZON AND LOCALITIES: Lower Bendigonian Be2. Known only from Allot. 16, Parish of Campbelltown, Victoria.

DIAGNOSIS: *Didymograptus* with narrow stipes having a semicircular curvature; initial angle of divergence 170° - 180° , distally 260° - 320° . Thecae simple conical tubes, apertural margins concave.

DESCRIPTION: The small sicula is 1 mm or slightly less long, and about 0.3 mm wide at the aperture. The stipes have a characteristic semicircular curvature, are rarely more than 5 mm long. Proximally the stipes



FIG. 4—*Didymograptus eocaduceus* (a) NV 13800 Lectotype. Allot. 16, Campbelltown, Victoria, $\times 7.5$. (b) GS 3682. Same locality as (a), $\times 7.5$. *Didymograptus hemicyclus* (c) NV 13797 Lectotype. Same locality as (a), $\times 3.75$. (d) GS 3706. Same locality as (a), $\times 3.75$. *Skiagraptus gnomonius* (e) SM A6338 Lectotype. Loc. Ba71, Gisborne, Victoria, $\times 7.5$. (f) SM A60285b Wileys Quarry, Macedon, Victoria, $\times 7.5$, figured Skevington (1968). *Skiagraptus* sp. (g) Daniels Harbour, Newfoundland, $\times 31$ approx., figured Whittington and Rickards (1969). *Skiagraptus gnomonius* (h) GS 4000 Anakie Gorge, Victoria, $\times 7.5$. (i) GS 4001 Little River Gorge, Brisbane Ranges, Victoria, $\times 3.75$. (j) GS 4002 Moorabool River, Sheoaks, Victoria, $\times 3.75$.

are 0.6 to 0.8 mm wide, distally 0.9 to 1.0 mm. Thecae are conical tubes with straight or slightly curved (concave downwards) ventral walls. Apertural margins are straight or slightly concave, and make an angle of a little more than 90° with the stipe axis. Thecal overlap is very low, it may be 0.1 and is never more than 0.35.

REMARKS: One of the more interesting aspects of this species is the nature of the thecae which are almost identical with those of *Didymograptus cuspidatus*, a form occurring very high in the Victorian sequence (Da3 Zone of *Diplograptus decoratus*). It has some resemblance to *Isograptus tenuis* notably in the curvature of the stipes and the general fragility of the rhabdosome. The thecae, however, are distinctly different.

Genus *Skiagraptus* Harris 1933

Skiagraptus gnomonicus (Harris and Keble) 1916

(Fig. 4e, f)

1916 *Diplograptus gnomonicus* n. sp. Harris and Keble in Harris (1933).

1924 *Diplograptus gnomonicus* H. and K. in Harris.

1933 *Skiagraptus gnomonicus* (H. and K.) Harris.

MATERIAL: The holotype cannot be located in any of the Victorian collections. Specimen SM No. A 6338 from locality Ba71, Gisborne, Victoria, is designated the lectotype and is figured here as Fig. 4c. SM No. A 60285b, figured Skevington (1968) from Wileys Quarry, Macedon, is figured as Figure 4f. Three other specimens GS 4000, 4001, 4002 have been examined and are figured (4h, i, j). Preserved as thin films on slate.

HORIZON AND LOCALITIES: This species has a long stratigraphic range, appearing at the top of the Castlemainian Ca2 and persisting to the top of the Darrwilian Da2. It has been recorded from Lancefield, Gisborne, the Castlemaine district, Brisbane Ranges and Macedon.

DIAGNOSIS: Rhabdosome scandent, biserial, dipleural, incipiently monopleural. Thecae short, distal thecae highly inclined, spacing 12-13 in 10 mm, overlap 0.8 to 0.9. Proximal thecae grow downwards, succeeding thecae horizontal, distal thecae reclined. Thecal apertures concave to convex. Proximal development, apparently dichograptid.

DESCRIPTION: The rhabdosome is small: usually 0.8 to 1.0 cm long and 2 mm wide. The sicula seems to be very short. A long virgula is invariably present, and this, in some cases, may be relatively thick. Thecae short, up to 2 mm wide, although usually slightly less; apertural margins are concave to convex, and are directed outwards. The prominent sharp denticles are directed downwards, although some are directed outwards.

REMARKS: Harris related this species to *Isograptus forcipiformis* deriving it from the latter by a continuation, and completion, of the 'conrescent tendency'. If *I. forcipiformis* is a true isograptid, and the evidence clearly demonstrates that it is, then such a relation-

ship cannot exist. Apart from the difference in proximal development, there is a marked difference both in the types of thecae, and thecal growth patterns. Moreover, as already noted, the stratigraphic relationship precludes any possibility of development of *S. gnomonicus* from *I. forcipiformis*.

Sub-family ISOGRAPTINAE (Harris) 1933

REVISED DIAGNOSIS: Rhabdosomes of two uniserial stipes diverging at more than 180°, the proximal thecae growing entirely downward and opening in this direction; later thecae reclined. Thecae of the *Didymograptus* type. Proximal development Isograptid (*gibberulus*) type.

Genus *Isograptus* Moberg 1892

TRANSLATION OF ORIGINAL DIAGNOSIS (from Bulman, 1932b): 'Two branched rhabdosome, both branches of which grow out bilaterally symmetrical from the sicula. Each branch considered by itself is not bilaterally symmetrically formed. The two impressions which one of these graptolites leaves on a shale surface and its counterpart always show in the matter of the proximal end (including the sicula) a somewhat different appearance. One can therefore distinguish a front and a back, and consequently also a right and a left branch'.

AMENDMENT OF DIAGNOSIS (Bulman, 1932b): 'One of the most important characteristics of this genus is the fact that the first stipe develops not from th¹¹ as in the Dichograptidae in general, but from th¹² via a second crossing canal. The first few thecae of both stipes grow entirely downwards, and the stipes, which are of considerable width at their origin taper gradually to their distal extremity'.

NOTE BY HARRIS (1933): 'The genus is here enlarged to include forms which are almost certainly related to *I. gibberulus* . . . The crucial test is probably the origin of the first stipe from th¹² instead of th¹¹ . . . Bulman's 'gradual tapering of the stipes' is almost certainly not of generic importance'.

REVISED DIAGNOSIS (Beavis, 1972): Rhabdosome didymograptid. Stipes reclined, angle of divergence always greater than 180°. Proximal development isograptid (*gibberulus*) type. Initial thecae straight, entirely pendent, later thecae reclined. Thecae of *Didymograptus* type, simple tubes, curved or straight.

REMARKS: The tapering of stipes, specifically mentioned by Bulman in his diagnosis is not, as Harris stated, of generic importance. Since tapering of stipes is probably a reflection of the differing growth direction of the thecae in the distal part of the stipe, it may be that the tapering is significant at the specific level. The initial development of the rhabdosome is of generic importance, and Harris' view that this is the 'crucial test' of the genus is quite valid.

Isograptus victoriae Harris 1933

(Fig. 5a-u)

1933 *Isograptus caduceus* var. *victoriae* Harris

1971 *Isograptus victoriae victoriae* Cooper

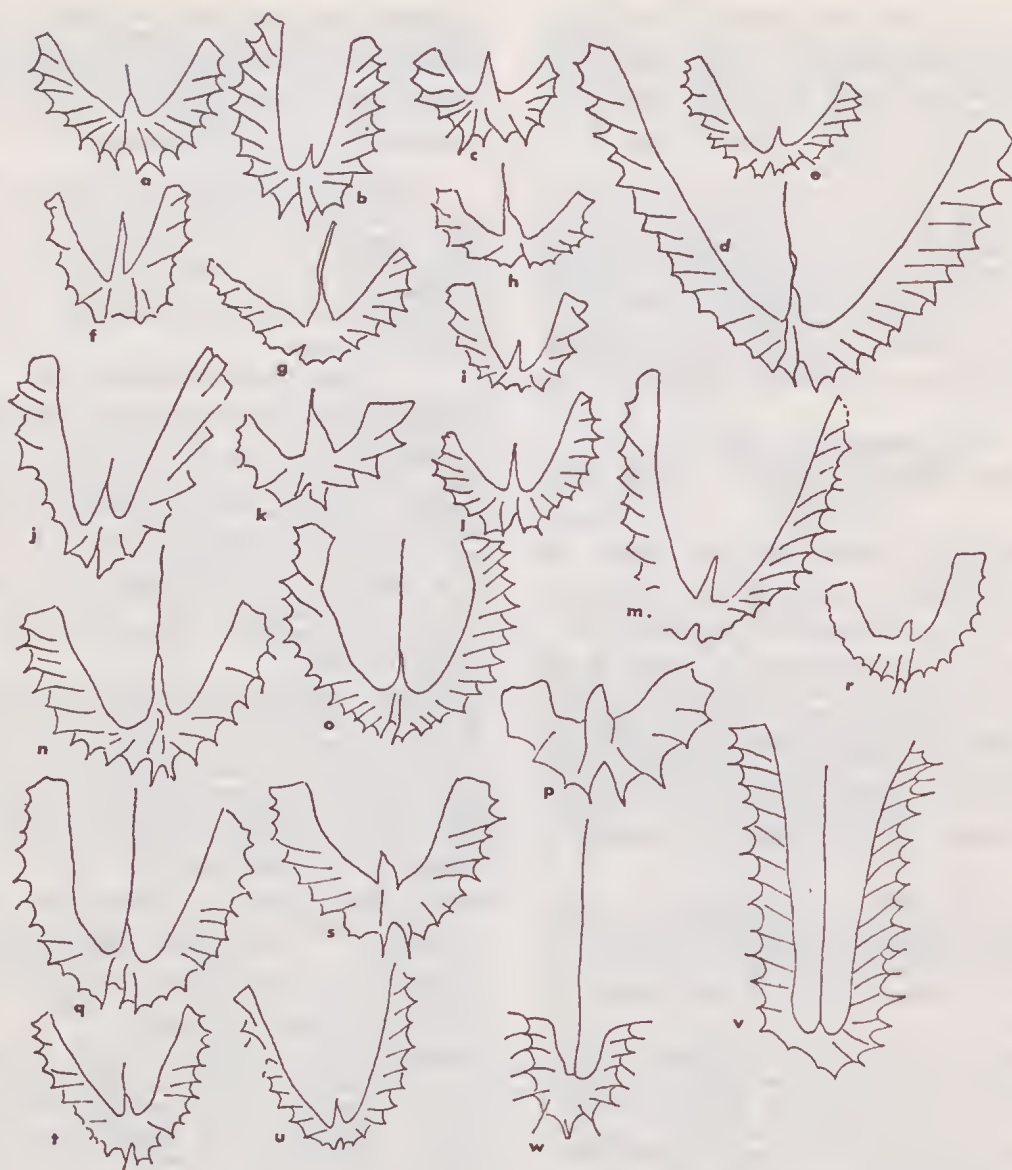


FIG. 5—*Isograptus victoriae* (a) SM A60286 Victoria Gully, Castlemaine, $\times 3$, figured Skevington (1965). (b) SM A6319a Victoria Gully, Castlemaine, $\times 3$. (c) SM A6319b Victoria Gully, Castlemaine, $\times 3$. (d) SM A6320 Between Rifle Range and township, Castlemaine, $\times 3$. (e) GS 4003 Durdidiwarrh Rd., Steiglitz, $\times 3$. (f) GS 4004 Durdidiwarrh Rd., Steiglitz, $\times 6$. (g) GS 4005 Old State School, Steiglitz, $\times 3$. (h) GS 4006 Old State School, Steiglitz, $\times 3$. (i) GS 4007 Mine dump, north of Steiglitz, $\times 3$. (j) GS 4008 Durdidiwarrh Rd., Steiglitz, $\times 6$. (k) GS 4009 Steiglitz, $\times 3$. (l) GS 4010 Sutherlands Ck, Steiglitz, $\times 3$. (m) GS 4011 *I. victoriae* - *I. maximus* transient, Yankee Gully, Steiglitz, $\times 3$. (n) GS 4012 *I. victoriae* - *I. maximus* transient, Grahames Gully, Durdidiwarrh, $\times 3$. (o) GS 4013 Durdidiwarrh Rd., Steiglitz, $\times 3$. (p) GS 4014 Durdidiwarrh Rd., Steiglitz, $\times 3$. (q) GS 4015 *I. victoriae* - *I. maximus* transient, Yankee Gully, Steiglitz, $\times 3$. (r) GS 4016 *I. victoriae* - *I. maximus* transient, Yankee Gully, Steiglitz, $\times 3$. (s) GS 4017 Brisbane Ranges, near Anakie North, $\times 3$. (t) GS 4018 *I. victoriae* - *I. maximus* transient, Yankee Gully, Steiglitz, $\times 3$. (u) GS 4019 Mariners Reef, Steiglitz, $\times 3$. (v) (w) Salter's original figures, enlarged $\times 3$ from *Quart. Jl. geol. Soc. London* 1853. '*Didymograptus caduceus*'.

MATERIAL: The figured specimens are SM No. A6319a, A6319b, A60286, Victoria Gully, Castlemaine, and SM No. A6320, between Military Rifle Range and Castlemaine. These are all catalogued as *Isograptus caduceus* var. *victoriae*. Specimens GS 400-4019, Steiglitz. Also figured are enlarged drawings of Salters' original figures (*Quart. Jl. Geol. Soc. London*, Vol. IX p. 87 Figure 1. 1853). In addition, approximately 250 examples were studied from GS, GV and NV collections. Specimen SM No. A 60286 is regarded as the typical example of the Victorian species.

HORIZON AND LOCALITIES: This is the zone fossil of the Castlemainian Ca2. It has a range from the base of this zone to the top of the Yapeenian zone Ya2. It occurs in the Castlemaine, Bendigo, Lancefield and Gisborne districts, in the Brisbane Ranges and the Mornington Peninsula.

REVISED DIAGNOSIS: Rhabdosome of two reclined stipes, dorsal walls slightly curved, diverging proximally at 250°, distally at 305° to 310°. Stipes about 1 cm long, but may be longer or shorter; 2.5 to 3.0 mm wide proximally, tapering to 2 mm or slightly less distally. Proximal thecae with gentle sigmoidal curvature, but th1¹ straight. Curvature decreases so that distal thecae are almost straight. Apertural margins concave, directed downwards in proximal thecae, outwards in others.

DESCRIPTION: The sicula is 4.5 to 5 mm long, and 1 mm wide at the aperture. A nema, sometimes quite long, is often attached. The sicula and th1¹ are in contact for almost the entire length, separation occurring in the apertural region so that there is a small n-shaped space between the apertural regions of the sicula and th1¹. The stipes are greatly curved giving a typical 'horse-shoe' shape to the rhabdosome. Gently tapering, the stipes have a width dis-

tally of 2 mm or slightly less, although rare specimens are as narrow as 1 mm.

The thecae are simple types: the proximal thecae are 2.0 mm long, 0.6 mm wide at the apertures; distal thecae are 1.2 to 1.5 mm long. Thecae number 11-12 in 10 mm; overlap is 0.9 or more.

REMARKS: Harris regarded this form (his var. *victoriae*) as the 'forma typica' of *Isograptus caduceus* in Victoria and it would appear that he regarded this, and *I. gibberulus* as conspecific. After a comparison of the Victorian *I. victoriae* and the European *I. gibberulus* (Table 7) the evidence points strongly to this being the case.

In *I. victoriae* the proximal thecae (except th1¹) are sigmoidally curved, with th1¹ and the distal thecae straight. Dorsal walls of the stipes are slightly curved. In *I. gibberulus* th1¹ and distal thecae are straight, the proximal thecae sigmoidally curved, or merely simply curved. Dorsal walls of the stipes are gently curved. In both, apertural margins are concave, directed downwards in the early thecae, and outwards in later thecae as the growth direction of the thecae changes from pendent to reclined. In both, denticles are prominent, directed downwards in the proximal thecae and outwards in the more distal. A study of Mobergs' and Elles' descriptions and figures show the same type and degree of variation in *I. gibberulus* as recorded by Harris for *I. victoriae*. The variation in the Victorian forms is illustrated by Fig. 5a, 5u.

Isograptus primulus Harris 1933

(Fig. 6a-d)

1933 *Isograptus caduceus* var. *primula* Harris

1971 *Isograptus victoriae primulus* Cooper

MATERIAL: Specimen GS No. 4021 figured here as Fig. 6b. Locality, mine dump near site of former

TABLE 7

	Stipe length Cm	Proximal width of stipe mm.	Distal width of stipe mm	Thecae in 10 mm	Divergence angle proximally	Divergence angle distally	Thecal overlap	Length of proximal thecae mm.	Length of distal thecae mm.	Width of proximal thecae mm.	Width of distal thecae mm	Apertural margins	Direction of denticle
<i>I. victoriae</i>	1+	2.5-3.0	2-	11-12	250°	305°-310°	0.9	2.0	1.2-1.5	0.6	0.5	Conc.	Out
<i>I. gibberulus</i>	1-2	2.5.	1+	13	260°	310°	0.9	2.0	1.3	0.7	0.5	Conc.	Out



FIG. 6.—*Isograptus primulus* (a) GS 4021 Birmingham Mine, Steiglitz, $\times 5$. (b) GS 4020 Steiglitz township, $\times 5$. (c) GS 4022/GV 7712 Steiglitz township, $\times 5$. (d) GS 4023 Mariners Gully, Steiglitz, $\times 5$. (e) *Isograptus lunatus* (e) GV 6923 Sutherlands Ck, Steiglitz, $\times 5$. (f) SM A6318 East of Victoria Gully, Castlemaine, $\times 5$. (g) GS 4024 Slate Quarry, Moorabool Rd., Meredith, $\times 5$. (h) GS 4025 Steiglitz, $\times 10$. (i) GS 4026 Durdidiwarrah, $\times 5$. (j) GS 4027 Durdidiwarrah, $\times 5$. (k) GS 4028 Durdidiwarrah, $\times 5$. (l) GS 4029 Durdidiwarrah, $\times 5$. (m) GS 4030 Durdidiwarrah, $\times 5$. (n) GS 4031 Durdidiwarrah, $\times 5$. (o) GS 4032 Durdidiwarrah, $\times 5$. (p) GS 4033 Durdidiwarrah, $\times 5$. (q) GS 4034 Durdidiwarrah, $\times 5$. (r) GS 4035 Durdidiwarrah Rd, Steiglitz, $\times 5$. (s) GS 4036 Durdidiwarrah Rd, Steiglitz, $\times 5$.



FIG. 7—*Isograptus maximus* (a) SM A6321c Bullengarook Slate Quarry, Gisborne, $\times 3$. (b) SM A6321a showing proximal region. Same locality as (a), $\times 25$. (c) SM A6321d showing proximal region. Same locality as (a), $\times 12.5$. (d) GS 4037 Moorabool River, Meredith, $\times 3$. (e) GS 4038 Sutherlands Ck, Steiglitz, $\times 3$. (f) GS 4040 Anakie Gorge, $\times 3$. (g) GS 4041 Moorabool River Bridge, Steiglitz-Meredith Rd, $\times 3$. (h) GS 4041 detail of proximal region, $\times 12.5$. (i) GS 4042 Steiglitz, $\times 3$. (j) GS 4043 Steiglitz, $\times 3$. (k) GS 4044 Yankee Gully, Durdidiwarrah, $\times 3$. (l) GS 4045 Grahames Gully, Steiglitz, $\times 3$. (m) GS 4045 detail of thecae, $\times 12.5$. (n) GS 4046 Yankee Gully, Steiglitz, $\times 3$. (o) GS 4047 Little River Gorge, Brisbane Ranges, $\times 3$. (p) GS 4048, Steiglitz, $\times 3$.

Steiglitz State School, Steiglitz, Victoria. Other material examined included 3 specimens from Steiglitz. All are preserved as white films on grey slate.

HORIZON AND LOCALITIES: Found as an important member of Chewtonian Ch2 and Castlemainian Ca1 assemblages: rare in Ca2 beds. Recorded from Castlemaine, Chewton, Bendigo, Brisbane Ranges and Steiglitz.

DIAGNOSIS: Rhabdosome of two stipes diverging initially at 180°, but distally 290° to 300°. Stipes taper rapidly so that distally they are about $\frac{1}{2}$ the width proximally. Apertural margins of thecae concave directed downwards in proximal thecae, outwards in distal thecae. Denticles small, directed downwards. Development isograptid (*gibberulus*) type.

DESCRIPTION: The sicula is long and narrow, 2.5 to 3 mm in length, apertural width 1 mm. The stipes are short, each stipe consisting of only about 4 thecae. Proximally the stipes are 2 mm wide, narrowing distally to 0.7 mm. The thecae are straight, simple tubes; proximal thecae are 1 mm long and 0.5 mm wide; distal thecae are 0.4 to 0.5 mm long. Thecal spacing is 10 to 12 in 10 mm, overlap 0.8 to 0.9.

Isograptus lunatus Harris

(Fig. 6e-s)

1933 *Isograptus caduceus* var. *lunatus* Harris

1971 *Isograptus victoriae lunatus* Cooper

MATERIAL: GV No. 6293, Sutherlands Creek. Steiglitz. Figured by Harris (1933) as Text figure 5, figured this paper as Fig. 6e. SM No. A 6318 is shown as Fig. 6f, east of Victoria Gully, Castlemaine. Other material examined: 11 specimens from Castlemaine, and 17 from Steiglitz. Of these GS 4024-4036 are figured. Preserved as thin films on grey slate.

HORIZON AND LOCALITIES: This species is the zone fossil for the Castlemainian Zone Ca1. It first appears at the top of the Chewtonian Ch2 and persists, with diminished importance to the Yapeenian Ya1. It has been recorded from Bendigo, Castlemaine, Chewton, Steiglitz, Brisbane Ranges and Mornington Peninsula.

DIAGNOSIS: Two uniserial reeined stipes of uniform width, with straight or uniformly curved dorsal walls, angle of divergence 295° to 310°. Thecae straight, simple tubes, apertural margins concave and directed upwards or outwards, but downwards on initial thecae. Development isograptid (*gibberulus*) type.

DESCRIPTION: The sicula is 1 mm long and 0.8 mm wide at the aperture. The stipes have a uniform width of 1.0 to 1.5 mm, length rarely exceeds 1 cm. The thecae are straight, 1.0 mm long and 0.6 mm wide at the aperture. Denticles are small but prominent. Thecal spacing varies from 14 in 10 mm in some examples to 11 in 10 mm in others. Overlap is more than 0.9. Distally, the thecal inclination becomes sharper; the fifth theca of each stipe is inclined at 95° to 100° to the stipe axis; the most distal thecae are inclined at less than 40°. In spite of this change, stipe width is uniform.

REMARKS: This species has a rhabdosome which is more robust and larger than that of *I. primulus*, while the angle of divergence is significantly greater. Later forms (from Ca2 to Ya1) tend to have larger rhabdosomes, but otherwise there is no marked difference.

Isograptus maximus Harris

(Fig. 7a-s)

1933 *Isograptus caduceus* var. *maxima* Harris

1971 *Isograptus victoriae maximus* Cooper

MATERIAL: SM No. A 6321e Bullengarook Slate Quarry, near Gisborne, Victoria, Fig. 7a, 3 specimens from Gisborne, SM collection; 16 from Steiglitz and 5 from Castlemaine, GV and GS collections. Preserved as white films on grey slate. Figured are SM No. A 6321a, d, GS 4037, 4038, 4040-4047.

HORIZON AND LOCALITIES: Zonal fossil for the Castlemainian Ca3, the form is equally prominent in Ca3 and Ya1 beds. It ranges up into the Darrwillian Da1. Recorded from Bendigo, Castlemaine, Gisborne, Macedon, Steiglitz, and Brisbane Ranges.

DIAGNOSIS: Rhabdosome two reclined stipes of uniform width with angle of divergence 300° to 310°. Stipes straight or with dorsal walls slightly curved. Thecae pendent in proximal region, distally reclined to scandent, curved; apertures concave, directed downwards in proximal thecae, outwards in distal thecae.

DESCRIPTION: The sicula may be 2.0 to 3.5 mm long and 1 mm wide, sometimes with a prominent nema. Two types are known: the large form (e.g. No. A 6321c) and the small form (e.g. SM No. A 6321b). In both the stipe width is about the same (1.5 to 2.00 mm) but in the large form, rarely less than 2.0 mm. The width of the stipe is constant throughout the rhabdosome. In the larger form, thecae are 4 mm long and 0.8 mm wide; in the smaller form, 2.5 mm long and 0.7 mm wide. In both forms, thecae number 11 to 12 in 10 mm with overlap 0.9 or more. The thecae are gently curved: curvature may be concave downwards or gently sigmoidal.

REMARKS: Of the two forms, the larger is the more common; both are quite distinct from *I. victoriae*. In particular, the stipes have a uniform width, and the thecae show distinct differences. It is quite clear in some examples (e.g. SM No. 6321a and A 6321d) that the proximal development is isograptid (*gibberulus*) type.

Isograptus maximodivergens Harris

(Fig. 8a-i)

1933 *Isograptus caduceus* var. *maximo-divergens* Harris

1971 *Isograptus victoriae maximo-divergens* Cooper

MATERIAL: Specimen SM No. A 6322a, Rifle Range, Castlemaine, figured here as Fig. 8a. Also figured are A 6322b from the same locality, and A 22750, Loc. Ba71 Gisborne. Other material examined: 21 specimens GS collection from Gisborne, Steiglitz and Castlemaine. Figured GS 4049-4053 from Steiglitz.

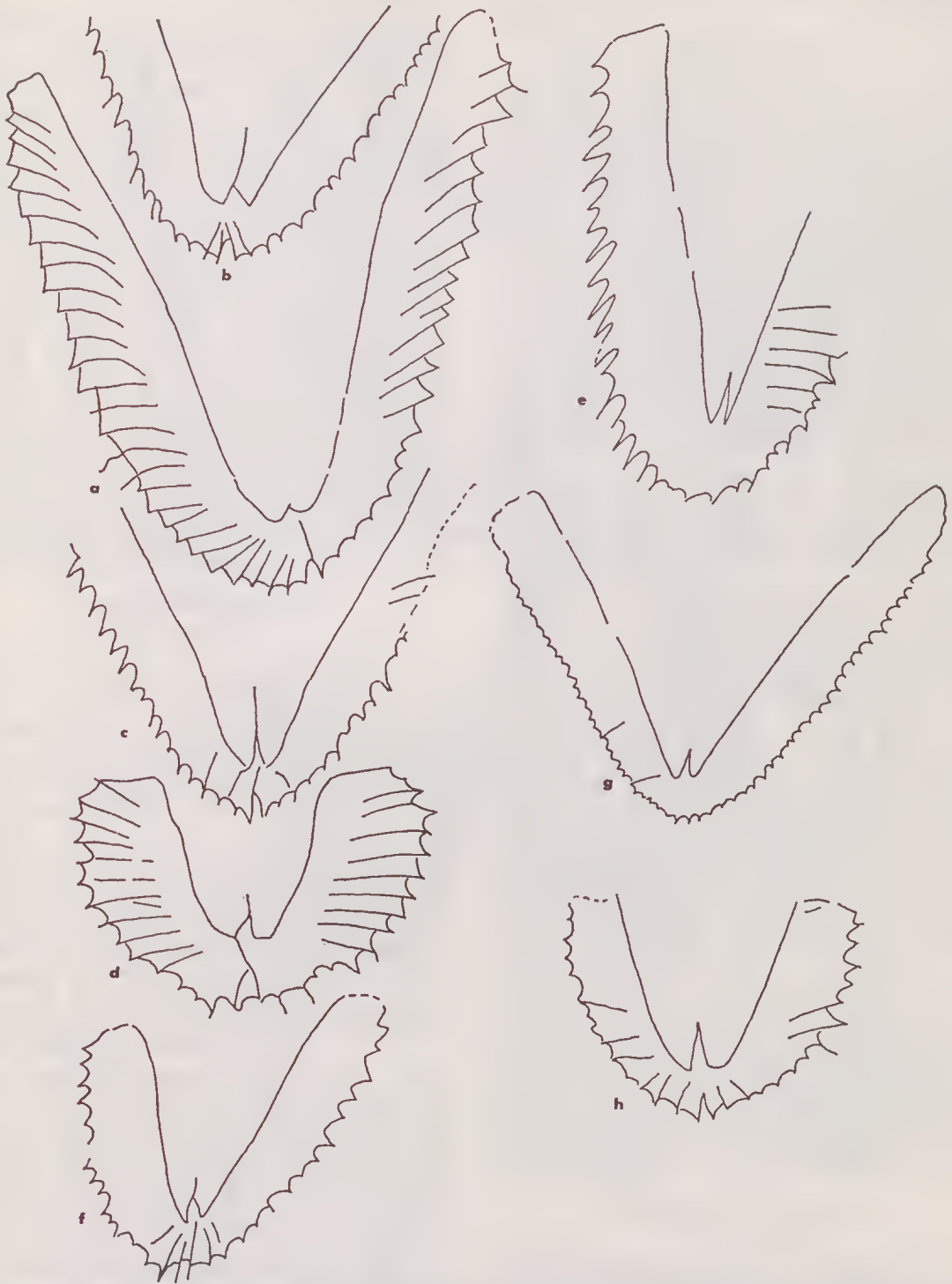


FIG. 8—*Isograptus maximodivergens* (a) SM A6322a Rifle Range, Castlemaine, $\times 3$. (b) SM A6322b Rifle Range, Castlemaine, $\times 3$. (c) SM A22750 Loc. Ba71, Gisborne, $\times 3$. (d) GS 4049 Steiglitz, $\times 3$. (e) GS 4050 Moorabool River, Sheoaks, $\times 3$. (f) GS 4051 Moorabool River Bridge, Steiglitz-Meredith Rd, $\times 3$. (g) GS 4052 Slate Quarry, Darragh, Meredith, $\times 1.8$ approx. (h) GS 4053 Same locality as (g), $\times 3$.

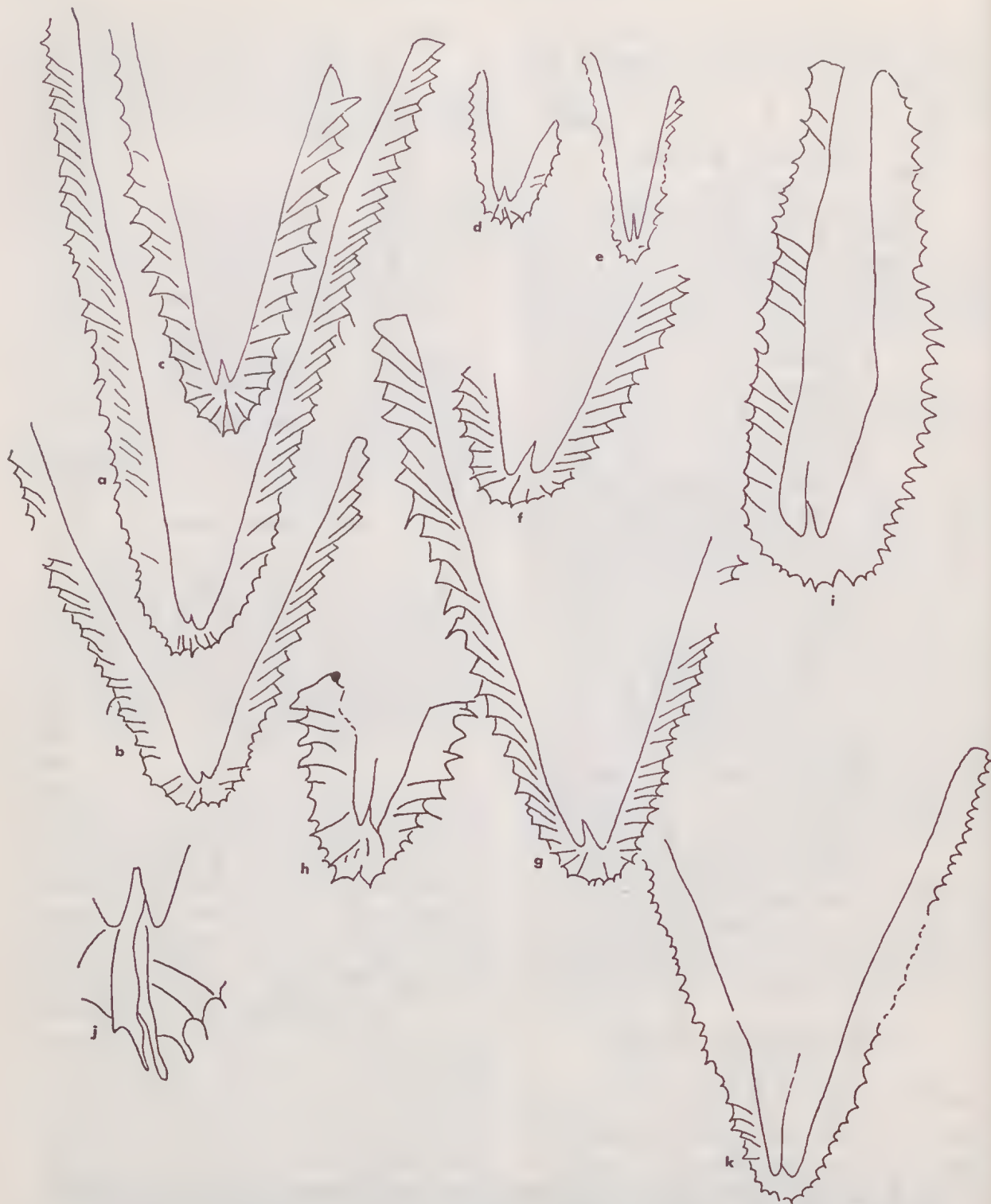


FIG. 9—*Isograptus divergens* (a) SM A6323a Chinamans Ck, Muckleford, $\times 2$. (b) SM A6323b Same locality as (a), $\times 2$. (c) GS 4054 Little River, Brisbane Ranges, $\times 3$. (d) GS 4055 Small form, Sutherlands Ck, Steiglitz, $\times 3$. (e) *? Isograptus divergens* (e) GS 4056 Similar to example figured by Harris (1933) as 'degenerate form'. Collected high Ca2 beds, Yankee Gully, Steiglitz, $\times 3$ (Darrwilian). (f) GS 4057 Cutting in Steiglitz-Maude Rd, south of Hanover Fault, $\times 3$. (g) GS 4058 Same locality as (f), $\times 3$. (h) GS 4059 Coolebarghurk Ck, Meredith, $\times 3$. (i) GS 4060 Brisbane Ranges, near Anakie Gorge, $\times 3$. (j) GS 4061 Same locality as (i), $\times 6$. (k) GS 4062 Moorabool River, Sheoaks, $\times 1.8$ approx.

HORIZON AND LOCALITIES: A typical Yapeenian form, this species first appears at the base of Ya1 and persists to the top of Darrwilian Da2. Recorded from Bendigo, Castlemaine, Macedon and Gisborne districts, the Brisbane Ranges and Steiglitz.

DIAGNOSIS: Two stipes reclined, angle of divergence 315° to 325°. Dorsal stipe walls straight or slightly curved. Stipes narrow in proximal region, widening at about the third theca in each stipe and then maintaining constant width. Thecae long, slightly curved.

DESCRIPTION: The sicula is 3 mm long, and 0.6 to 0.75 mm apertural width. A nema is usually present. Stipes are 2.5 to 3 cm long, 2.5 mm wide proximally widening to about 4 mm at about the third theca on each stipe. Some examples show a narrowing in the extreme distal region, but normally after widening, width is constant. Thecae are 4 mm long and 1 mm wide, but the first 2 or 3 thecae on each stipe are shorter. Thecae are simple, straight or with gentle curvature, concave downwards. Denticles are prominent and are directed downwards on the curved thecae, outwards on the straight. Thecae number 8 to 9 in 10 mm, and overlap is almost complete.

Some forms are known with stipes much longer than the figured examples: some are known with stipes 5 cm long and 5 mm wide.

Isograptus divergens Harris

(Fig. 9a-k)

1933 *Isograptus caduceus* var. *divergens* Harris

1971 *Isograptus victorae* *divergens* Cooper

MATERIAL: SM No. A6323a and A6323b, Chinamans Creek, Muckelford. These examples are preserved as limonite films on fawn slate. Other material examined: 7 specimens as white films on black slate, GS collection, Steiglitz. Of these GS 4050-4062 are figured.

HORIZON AND LOCALITIES: This form is present in Yapeenian Ya1 and Ya2 assemblages. It persists in diminishing importance to the top of Darrwilian Da3. Recorded from Bendigo, Castlemaine, Gisborne and Macedon districts, Steiglitz, and Brisbane Ranges.

DIAGNOSIS: Two stipes diverging at 330° to 335°. Stipes show slight distal tapering; dorsal walls straight or slightly curved. Thecae curved or straight, number 10 to 11 in 10 mm, overlap 0.8 to 0.9.

DESCRIPTION: The sicula is relatively small: 2.5 to 3 mm long with an apertural width of 1 mm. The stipes are up to 6 cm long and 2.0 to 2.5 mm wide. The dorsal stipe walls may be straight, but more commonly they have a gentle irregular curvature. The thecae are 3.0 to 3.5 mm long and 0.9 mm wide, although they may be narrower. They are simple tubes, straight, or with a slight downwardly concave curvature. The apertural margins are straight and make an angle of 90° or more with the ventral thecal wall.

REMARKS: The stipes in this species are relatively narrower than those of *I. maximodivergens*. Harris described the rhabdosome as being 'less robust' than that of *I. divergens*. The dimensions given above are

typical, but both larger and smaller examples have been recorded.

Isograptus imitatus Harris

(Fig. 10a-c)

1933 *Isograptus caduceus* var. *imitata* Harris

MATERIAL: SM No. A60288, Fitzgeralds Quarry, Gisborne, figured Skevington (1968) and figured here as Fig. 10a. Also figured are A60287 from the same locality, also figured by Skevington (1968) and figured here as Fig. 10b. Also figured are A60287 from the same locality, also figured by Skevington (1968) and A 60234 Bullengarook Slate Quarry, Gisborne. All are preserved as white films on black slate. In addition to the figured material, three specimens from Muckelford, Victoria, were examined.

HORIZON AND LOCALITIES: This species first appears near the top of the Castlemanian Ca3 and persists into the basal beds of the Darrwilian Da1. Recorded from Gisborne and Castlemaine (Muckelford) districts.

DIAGNOSIS: Two reclined stipes, near scandent, diverging at 325° to 330°. Sicula very long and narrow. Thecae curved, more so proximally than distally. Proximal thecae pendent and almost straight, distal thecae reclined.

DESCRIPTION: In the few specimens examined there appears to be considerable variation, but some features are relatively constant. The sicula is long, 8 mm or more, and narrow, with an apertural width of 1 mm. There is frequently a long nema. The stipes vary in length, maximum 1.5 cm. They are widest in the proximal region (3 to 3.5 mm) narrowing to 2.2-2 mm distally. Thecae are 1.5 mm long and 0.5 mm wide, number 8 to 10 in 10 mm and overlap 0.95 to 1.0. The first two thecae of each stipe have apertures opening downwards; the intermediate thecae open outwards, and the distal thecae upwards. The denticles are very prominent and are directed downwards or outwards. It is characteristic of this species, as for *I. victorae* that th1¹ and the sicula, in contact for almost their entire length, separate aperturally, so that there is between the apertures of the two, a n-shaped space.

REMARKS: Harris regarded this species as a catagenetic variety of *I. caduceus* and considered that it resembled the much earlier *I. lunatus*. However, it has a much more robust rhabdosome and the morphology of the proximal region is quite distinct. Harris erred in stating the *I. imitatus* persists into the Upper Ordovician. There is no record, so far as can be ascertained, of it in beds higher than the lowest Darrwilian.

Isograptus velatus Harris

(Fig. 10d, e)

1933 *Isograptus caduceus* var. *velata* Harris

MATERIAL: GV No. 31331. Locality L34, Lancefield, figured here as Fig. 10d. Also figured is SM No. A6323d Muckelford, which may be a juvenile form of this species, or may be a juvenile *Pseudisograptus*.

HORIZON AND LOCALITIES: A very rare Yapeenian form, known with certainty only from Lancefield.

DIAGNOSIS: Two tapering stipes diverging at 330° - 340° , dorsal walls gently curved. Thecae straight to slightly curved, apertural margins straight to slightly concave, directed outwards even in the proximal thecae. Proximal development modified isograptid (*gibberulus*) type.

DESCRIPTION: The sicula is 2.5 mm long. The stipes taper from a width of about 2 mm proximally to 1.0 mm distally. The stipes are 5 mm long. Proximal thecae are 1.5 mm long, distal thecae 0.9 mm, width of thecae is 0.6 to 0.7 mm. Thecae number 9 to 10 in 10 mm, overlap 0.6.

REMARKS: Certain features of this species suggest that it has affinities with *Pseudisograptus*: notably the outward direction of apertures of $th1^1$ and $th1^2$. However, with only one certain specimen of this form, reference to the genus *Pseudisograptus* could not be justified at this stage.

Isograptus tenuis Harris

(Fig. 10f)

1933 *Isograptus caduceus* var. *tenuis* Harris

MATERIAL: Two specimens GS 4063, 4064 preserved in white on pale slate.

HORIZON AND LOCALITIES: A rare form known only from Locality Ba67, Gisborne. Upper Ordovician, it does not have the range Castlemainian to Upper Ordovician given by Harris.

DIAGNOSIS: Small rhabdosome with slender stipes diverging at 300° . Thecae simple straight tubes, apertural margins straight. Denticles weak.

DESCRIPTION: The stipes are 6 mm long, and 0.6 mm wide. The sicula, 1 mm long, is not prominent. The thecae are simple straight tubes, 0.7 mm long and 0.4 mm wide, number 12 to 14 in 10 mm, overlap 0.4. Apertural margins are directed outwards.

Isograptus ovatus (T. S. Hall)

(Fig. 11a, b)

1902 *Didymograptus ovatus* T. S. Hall

1933 *Isograptus ovatus* Harris

MATERIAL: A single complete specimen, the lectotype, SM No. A 6345, 'The 8 Mile', Howqua River. Preserved as a fine film on black slate, and one incomplete specimen from Moorabool River, Steiglitz (GS 4039).

HORIZON AND LOCALITIES: A very rare form found from the base of the Yapeenian Ya1 to the base of Ya2. Known from 6 examples only: Tabberabbera (1) Turners Quarry, Bittern (2), 'The 8 Mile', Howqua (2), Steiglitz (1).

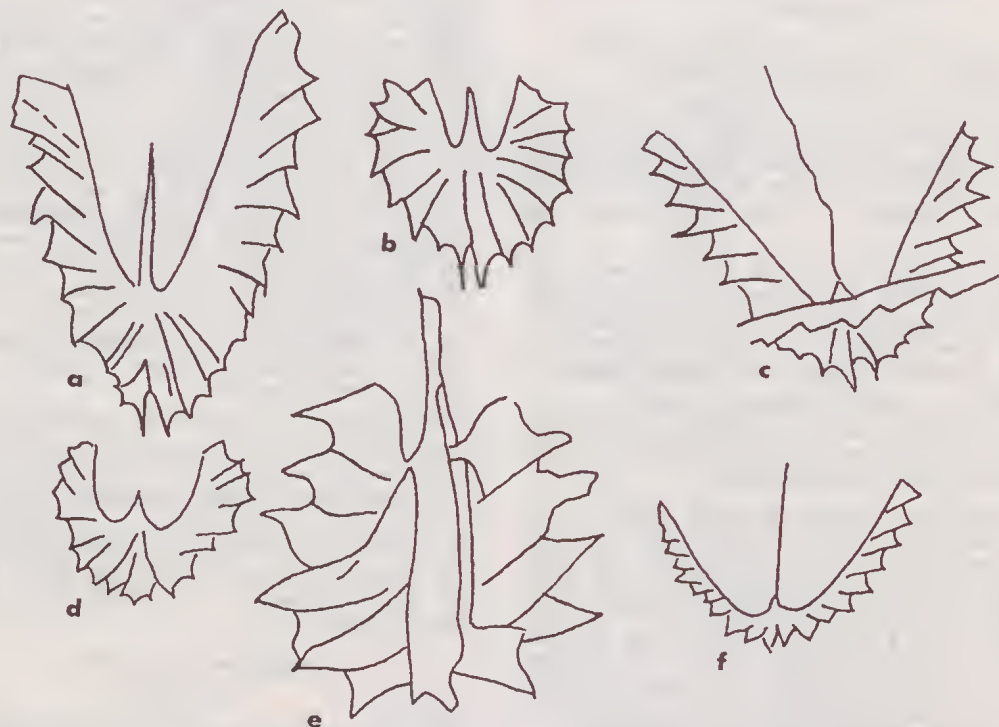


FIG. 10—*Isograptus imitatus* (a) SM A80288 Fitzgeralds Quarry, Gisborne, figured Skevington (1968), $\times 4$. (b) SM A60287 Same locality as (a), figured Skevington (1968), $\times 4$. (c) SM A60234, Bullengarook Slate Quarry, Gisborne, $\times 4$. *Isograptus velatus* (d) GV 31331 Lectotype, Lancefield, $\times 4$. ? *Isograptus velatus* (e) Juvenile form SM A6323d Chinamans Ck, Muckleford, $\times 8$. *Isograptus tenuis* (f) GS 4063 Lectotype. Loc. Ba67, Gisborne, $\times 4$.

REVISED DIAGNOSIS: Two scandent stipes, uniform in width, with curved dorsal margins, converging distally. Thecae curved, with strongly concave apertural margins.

DESCRIPTION: The sicula is 3.5 mm long and is narrow. The stipes are 1 cm long, with uniform width of 1.8 mm. Thecae are curved, 1.5 mm long, 0.5 mm wide. Thecal spacing is 12 in 10 mm with overlap 0.5 or slightly more.

REMARKS: This rare form is noted for the distinctive ovate outline of the rhabdosome. The rather thick sicular region is the only basis for regarding it as related to *Pseudisograptus*; at present there is inadequate data to warrant reference of the form to this genus.

***Isograptus forcipiformis* Ruedemann**
(Fig. 11a-i)

1904 *Isograptus forcipiformis* Ruedemann (1904)

1933 *Isograptus forcipiformis* Harris (1933)

1968 *Isograptus forcipiformis* Skevington (1968)

MATERIAL: Fourteen examples from Strathfieldsaye, near Bendigo preserved as purple films on fawn slate; three from Steiglitz preserved as carbonaceous films on brown shale.

HORIZON AND LOCALITIES: Base of Yapeenian Ya1 to the top of Darriwilian Da3. It is most common in this upper zone. It has been recorded from the Bendigo, Gisborne and Steiglitz districts.

DESCRIPTION: The rhabdosome consists of two scandent stipes with dorsal margins straight and parallel. The stipes are 0.7 to 1.5 cm long and 1.0 to 1.2 mm wide. In the proximal region the stipes may be up to 4 mm wide. Distance between the dorsal walls of the two stipes is 0.8 to 1.2 mm. The sicula is up to 5 mm long and is narrow. Thecae are about 1 mm long, apparently 0.4 mm to 0.5 mm wide, but possibly wider (see 'Remarks'). Thecae are curved, but the curvature decreases in the distal thecae. Apertures generally concave, directed outwards, or in some examples, those of the distal thecae may be directed upwards. Denticles pronounced, directed downwards. Thecae number 9-11 in 10 mm, overlap almost complete.

REMARKS: Ruedemann regarded this species as an extreme development of *I. caduceus* in its divergence and the slenderness of the stipes. Harris regarded it as the final stage before concrescence to produce *Skiagraptus*. This view is now untenable on both palaeontological and stratigraphic evidence, although in one example (e.g. Fig. 11d) there are some



FIG. 11—*Isograptus ovatus* (a) SM 6345 'The 8 Mile', Howqua, $\times 3$. (b) GS 4039 Moorabool River Bridge, Steiglitz-Meredith Rd, $\times 3$. *Isograptus forcipiformis* (c) SM A6341 Strathfieldsaye, $\times 3$. (d) SM A60291 Jacksons Ck, Gisborne, $\times 6$. (e) SM A60290a Strathfieldsaye, $\times 3$. (f) GS 4065 Steiglitz-Maude Rd, $\times 3$. (g) GS 4066 Same locality as (f), $\times 3$. (h) GS 4067 Moorabool River, Sheoaks, $\times 3$. (i) GS 4068 Road cutting south of Hanover Fault, Steiglitz-Maude Rd, $\times 3$.

skiagraptid aspects in the proximal region, particularly in the outward direction of growth of the th^{11} . However, the proximal development is clearly isograptid, though of a modified type. Lacking any definite evidence to justify reference to another genus, this form is here retained in the genus *Isograptus*.

One interesting feature of this species is the incipient monopleurial arrangement of the thecae, with a distinct lateral overlap shown in the highly compressed specimens as a very dark and slightly thicker band of limonite. With this arrangement, in vertical plan the rhabdosome would have a broad, open shape.

***Isograptus pertensus* Harris**

(Fig. 12a-f)

1933 *Isograptus caduceus* var. *pertensa* n. var. Harris

1968 *Isograptus pertensa* Beavis and Beavis

MATERIAL: Lectotype GV No. 6719 Sutherlands Creek, Steiglitz. Preserved as white film on black, strongly cleaved slate. Seven other specimens from the same locality and four from the Moorabool R.

Sheoaks, downstream of Coolebarghurk Creek Junction.

HORIZON AND LOCALITIES: Range from transitional Ca3-Ya1 beds to Darriwilian D4. Known only from Steiglitz and a small form from Lancefield.

DIAGNOSIS: Two long, slender, scandent stipes diverging at 340° . Stipes straight to gently curved, tapering distally. Thecae small, simple; apertural margins concave, denticles small.

DESCRIPTION: Rhabdosome large, with stipes up to 10 cm long; proximally 3 mm wide, distally 1.5 mm. The sicula is small: 8 mm long and less than 1 mm wide at the aperture. Proximal thecae 7 to 8 in 10 mm, 4 mm long, 0.8 mm wide, strongly denticulate. Distal thecae 6 to 7 in 10 mm, smaller, less denticulate. Overlap almost complete.

REMARKS: A small form, identical in all respects except size, has been recorded from the Lancefield district. Harris referred to this as *I. caduceus* var. *horrida* but there seems no justification for regarding

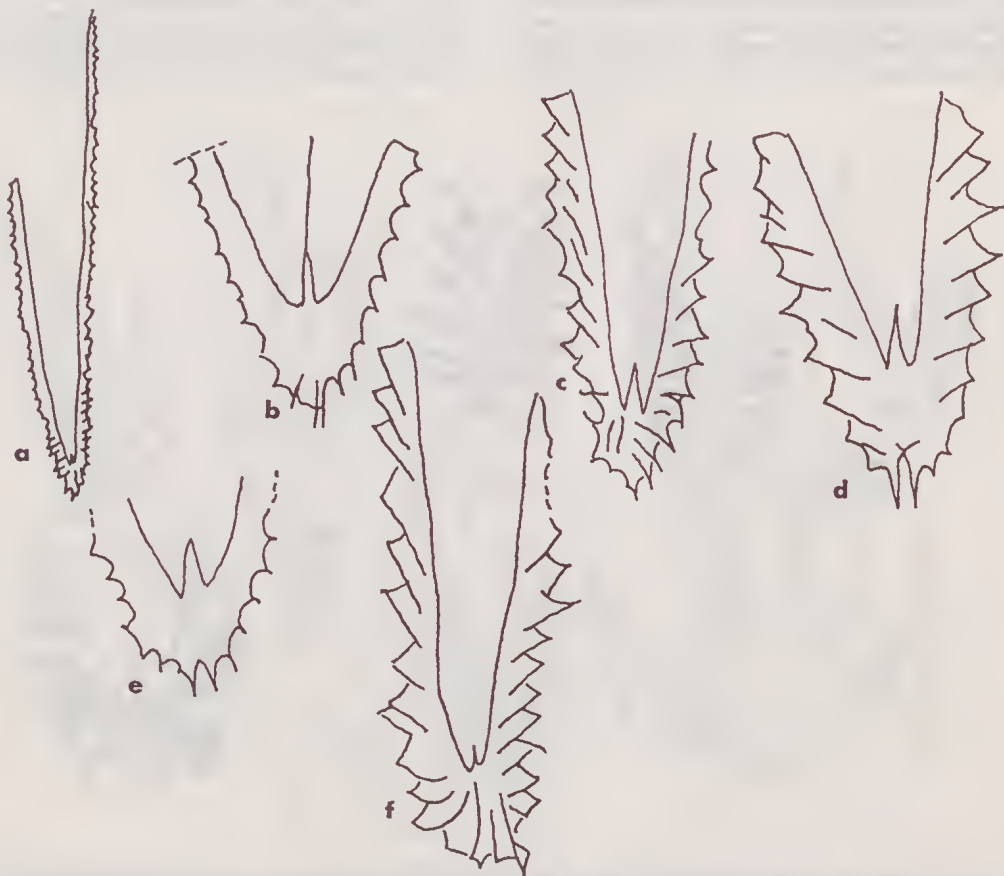


FIG. 12—*Isograptus pertensus* (a) GV 6719 Lectotype. Sutherlands Ck, Steiglitz, $\times 0.7$ approx. (b) GS 4069 Coolebarghurk Ck, Meredith, $\times 4$ approx. (c) GS 4070 Moorabool River, Sheoaks, $\times 4$ approx. (d) GS 4071 Same locality as (c), $\times 4$ approx. (e) GS 4072 Anakie Gorge, $\times 4$ approx. (f) GS 4073 Collected from type locality at point where Hanover Fault is crossed by Sutherlands Ck, near Mariners Gully, $\times 4$ approx.

it as a separate form. *I. pertensus* is notable for the relatively primitive thecae, reminiscent of some of the lower Castlemainian forms; Harris regarded it as a catagenic variety of *I. caduceus*.

Isograptus harrisi n. sp.

(Fig. 13a,e)

MATERIAL: Holotype GS 4075. Maude Road, Steiglitz. Fifteen other specimens from the same locality of which four are figured.

DERIVATION OF NAME: Named for the late Dr. W. J. Harris.

HORIZON AND LOCALITIES: Darriwilian, Da1. Known from Maude Road, Steiglitz, where beds are exposed in a road cutting about 1.5 km south of Steiglitz cemetery. Also collected on Coolebarghurk Creek near Meredith.

DIAGNOSIS: Small *Isograptus* with long prominent sicula. Stipes taper slightly. Thecae simple, with high overlap. Proximal development isograptid (*gibberulus*) type.

DESCRIPTION: The sicula is relatively long (3.6 mm including ventral process) and narrow, 0.7 mm at aperture. Th1¹ arises high up on the sicula and grows down along, and apparently in contact with, the sicula for its entire length. Th2¹ appears to rise high up on th1¹ at first and then curve outwards. Thecae are simple, overlap 0.85 to 1.0, dorsal walls slightly curved, apertural margins concave, sometimes with a fine denticle. Apertures of proximal thecae directed downwards or slightly outwards; all other thecae have apertures directed outwards. Thecae number 13-15 in 10 mm. Initially the stipes are 1.8 mm to 2.0 mm wide, but taper rapidly to 0.8 to 0.9 mm. Dorsal walls are curved. Initially the angle of divergence is 180°; distally it may be as high as 330°. The rhabdosome is small, usually 4 mm or less wide.

REMARKS: This small form occurs relatively abundantly

at the type locality but is rare at the other locality from which it was recorded. Both localities are high Da1 transitional to Da2, with *Glyptograptus austrodentatus*, *G. intersitus*, *Paraglossograptus etheridgei* and *Tristichograptus ensiformis* as associates.

The proximal development is almost certainly of the isograptid (*gibberulus*) type, although some curvature of the distal parts of the proximal thecae is a modification of this type. The form is morphologically quite distinctive from other Darriwilian isograptids.

Sub-family CARDIOGRAPTINAE Mu and Zhan 1966

Genus *Oncograptus* T. S. Hall 1914

Oncograptus upsilon T. S. Hall

(Fig. 14a-i)

1914 *Oncograptus upsilon* T. S. Hall

MATERIAL: Three specimens of the subspecies *O. upsilon biangulatus* preserved in relief from the El Paso Limestone, Texas. Twenty-two compressed specimens from Victoria: brown or white films on dark slate.

HORIZON AND LOCALITIES: Zonal fossil for the Yapeenian Ya1. The species ranges up into Ya2. The subspecies *O. upsilon biangulatus* Harris and Keble is an upper Ya1-lower Ya2 form. Occurs at Bendigo, Castlemaine, Gisborne, Macedon, Mornington Peninsula, Brisbane Ranges, Steiglitz. In the Brisbane Ranges it has been recorded from Da1 beds.

DESCRIPTION: Rhabdosome initially biserial, distally consisting of two uniserial stipes. The biserial part of the rhabdosome is 1.5 to 2 cm long, and with a maximum width of 1.3 cm at the bifurcation. It is 4 to 5 mm wide proximally. The uniserial stipes are of uniform width, up to 5 mm and may be 2 cm long. Thecae in the biserial part of the rhabdosome are 5 mm long and 1 mm wide and are sigmoidally curved



FIG. 13—*Isograptus harrisi* (a) GS 4075 Holotype. New road cutting on Steiglitz-Maude Rd, 1.5 km south from new Steiglitz cemetery, $\times 9$. (b) GS 4074 Same locality as (a), $\times 9$. (c) GS 4076 Same locality as (a), $\times 9$. (d) GS 4077 Same locality as (a), $\times 4.5$. (e) GS 4078 Coolebarghurk Ck, Meredith, $\times 4.5$.



FIG. 14—*Oncograptus upsilon* (a) SM A22748 Loc. Ba71, Gisborne, $\times 3$. (b) SM A 6325 Bullengarook Slate Quarry, Gisborne, $\times 3$. *Oncograptus upsilon biangulatus* (c) SM A6333 Loc. Ba71, Gisborne, $\times 3$. (d) SM A8140 Detail of bifurcation, El Paso, Texas, figured Bulman (1936), $\times 3$. *Oncograptus upsilon* (e) GS 4079 Moorabool R. Bridge, Steiglitz-Meredith Rd. Detail of bifurcation, $\times 3$. (f) GS 4080 Moorabool River, east from Meredith, $\times 1.75$ approx. (g) GS 4081 Meredith Rd, Steiglitz, $\times 3$. *Oncograptus upsilon biangulatus* (h) GS 4082 Little River, Brisbane Ranges, $\times 3$. *Oncograptus upsilon* (i) GS 4083 Moorabool River, Steiglitz, $\times 3$.



FIG. 15—*Cardiograptus morsus* (a) SM A6323c Chinamans Ck, Muckleford, $\times 3$. (b) GS 4084 Moorabool River, Sheoaks, $\times 3$. (c) GS 4085 Moorabool River, Sheoaks, $\times 3$. (d) GS 4086 Anakie Gorge, $\times 3$. (e) GS 4087 Same locality as (d), $\times 3$. (f) GS 4088 Same locality as (d), $\times 3$. (g) GS 4089 Same locality as (d), $\times 3$. (h) GS 4090 Little River, Brisbane Ranges, $\times 3$. (i) GS 4091 Moorabool River Bridge, Steiglitz-Meredith Rd, $\times 3$. (j) GS 4092 Preserved on relief in pyrite. Sicular region. Coolebarghurk Ck, Sheoaks, $\times 6$. *Cardiograptus crawfordi* (k) SM A60280 Strathfieldsaye, $\times 6$.

with overlap complete. They number 12 to 13 in 10 mm. Apertural margins are concave, and well developed denticles are present.

The uniserial stipes have straight or slightly curved dorsal margins and diverge at 330° . The thecae are curved, but much less so than in the biserial portion. Thecae number 10 in 10 mm are 4 mm long, 0.8 to 1.0 mm wide, overlap 0.85 to 1.0.

REMARKS: The length of the uniserial stipes does not appear to be significant and can vary considerably. The subspecies *O. upsilon biangulatus* H. and K. is always less than 1 cm wide at the bifurcation. The uniserial stipes have a greater angle of divergence (335° to 340°) and the uniserial stipes are always less than 5 mm wide. Thecae on the two forms are identical.

Genus *Cardiograptus* Harris and Keble 1916

Cardiograptus morsus H. and K.

(Fig. 15a-j)

1916 *Cardiograptus morsus* Harris and Keble in Harris

MATERIAL: Two specimens from Chewton, 17 specimens from Steiglitz and 1 specimen from Muckleford.

One specimen from Steiglitz (Fig. 15j) preserved in pyrite, is the first example known which gives some indication of the proximal development.

HORIZON AND LOCALITIES: Zonal fossil of the Yapeenian Ya2. Range from the top of Ya1 to the top of Ya2. It is a short lived species. Recorded from Bendigo, Castlemaine, Gisborne, Steiglitz and Brisbane Ranges.

DESCRIPTION: Rhabdosome biserial throughout, up to 2 cm long and 3 mm wide proximally. The rhabdosome broadens to about 11 mm, at about $\frac{2}{3}$ the length of the rhabdosome and then tapers to about 9 mm distally. In the narrow form of this species, the dimensions are length 8 to 9 mm, proximal width 2 mm, width at $\frac{2}{3}$ length 4 mm, and width distally 3.5 mm.

Proximally, the thecae are strongly curved, but in distal thecae, curvature decreases. Apertural margins are straight to concave and denticles pronounced. The thecae number 10 in 10 mm with overlap 0.95.

Along the rhabdosome there is a progressive change in the direction of thecal growth: proximal thecae grow entirely downwards, but after the fifth, the thecae are horizontal and ultimately the south direction is upwards, so that distal thecae make a

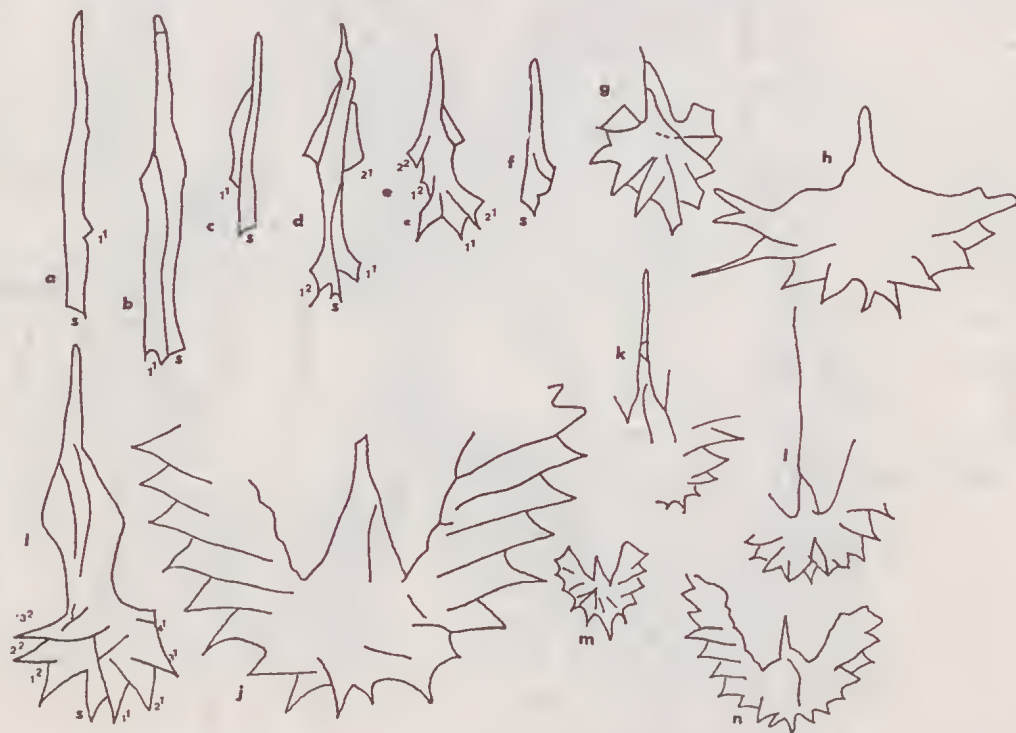


FIG. 16—*Pseudisograptus manubriatus*. All specimens from Wileys Quarry, Macedon. (a)-(i) Growth stages. SM A60281a, A60281b, A60281c, A60281e, A6351a, A6348a, A60281g, A60281a(i), A60282a, $\times 6$. (j) Complete rhabdosome SM A6348b, $\times 6$. (k) Proximal region SM A6327b, $\times 6$. (l) Proximal region SM A6327b, $\times 6$. (m) Small form SM A60284d $\times 3$, figured Skevington (1968). (n) Normal form SM A60284b $\times 3$, figured Skevington (1968).

sharp angle with the axis of the rhabdosome. Some specimens have a prominent virgula-like structure.

***Cardiograptus crawfordi* Harris**

(Fig. 15k)

1926 *Cardiograptus crawfordi* Harris 1926

MATERIAL: Three specimens from Bendigo East. Preserved as purple films on pink slate.

HORIZON AND LOCALITIES: Darriwilian Da2 to Da3. Known only from Bendigo East.

DESCRIPTION: Rhabdosome biserial, 8 to 10 mm long and tapering from a width of 5 mm distally to 1.5 mm proximally. Thecae have concave apertural margins, with pronounced denticles directed downwards. Thecae number 11 to 13 in 10 mm, overlap 0.98 to 1.0. Proximal thecae pendent, and gradually direction of growth changes so that th is horizontal and subsequent thecae reclined.

REMARKS: The form is small, and is readily distinguished from *C. morsus*. The central virgula is particularly strong. Thecae are relatively shorter and broader than in *C. morsus*.

Family SINOGRAPTIDAE Mu 1957

Genus *Pseudisograptus* Beavis 1972

Pseudisograptus manubriatus (T. S. Hall)

(Fig. 16a-n, 17a-l)

1914 *Didymograptus caduceus* var. *manubriatus* T. S. Hall

1933 *Isograptus manubriatus* Harris

1968 *Maeandrograptus manubriatus* Skevington

1972 *Pseudisograptus manubriatus* Beavis

MATERIAL: Hall's type specimen is missing. The specimen of Hall Fig. 12 (T. S. Hall, 1914), nominated as lectotype by Harris (1933) by publication when the second syntype was removed to a new

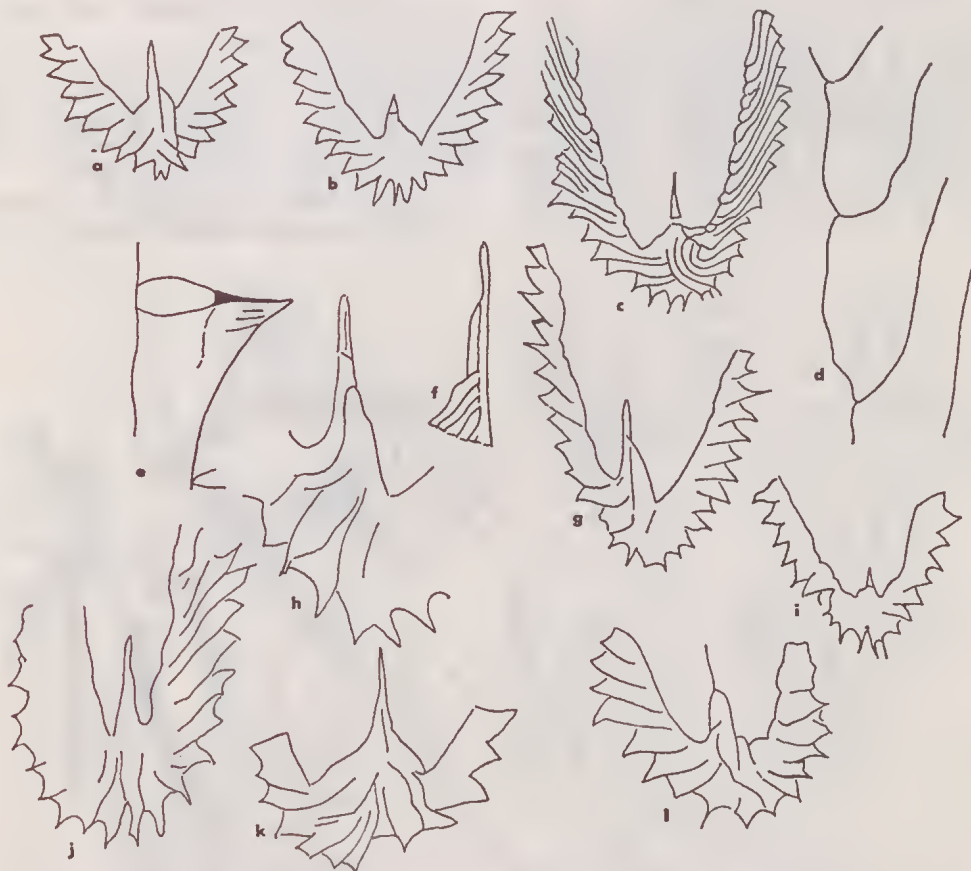


FIG. 17—*Pseudisograptus manubriatus* (a) SM A60284a, Wileys Quarry, Macedon, figured Skevington (1968), $\times 3$. (b) SM A60284c Wileys Quarry, Macedon, figured Skevington (1968), $\times 3$. (c) SM A603142 Marathon, Texas, figured Bulman (1968), $\times 3$. (d) SM A603142 Marathon, Texas, showing prothecal folds, $\times 25$. (e) SM A603142 showing thecal aperture, $\times 25$. (f) SM A603142 showing apical portion of sicular, $\times 12.5$. (g) GS 4093 Moorabool River, Sheoaks, $\times 3$. (h) GS 4093 showing proximal region, $\times 6$. (i) GS 4094 Moorabool River, Sheoaks, $\times 3$. (j) GS 4095 Moorabool River, Sheoaks, small form, $\times 6$. (k) GS 4096 Moorabool River, Sheoaks, $\times 6$. (l) GS 4097 Steiglitz-Maude Rd, $\times 6$.

species. The figured specimen of Harris (NV No. 13803) is imperfect; specimen SM No. A 6348b; and 72 examples from Wileys Quarry, Macedon, Victoria all preserved as film on black slate; 30 specimens, similarly preserved, from Steiglitz and specimen SM No. A603142 from Marathon, Texas, preserved in relief. In addition, uncatalogued material from Newfoundland, being studied by research students at Cambridge, was examined.

HORIZON AND LOCALITIES: Restricted to Yapeenian Ya1 and Ya2. The form has been recorded from Macedon, Gisborne, Castlemaine and Steiglitz.

REVISED DIAGNOSIS: Rhabdosome of two stipes diverging initially at 130° to 140° , but after the third theca on each stipe, at 300° . Initial thecae grow downwards and then curve outwards. Thecae long, with simple prothecal folds, imparting an undulate dorsal margin to the stipes. Initial thecae proliferate in the sicular region.

DESCRIPTION: The sicula is long; almost 1 cm in some specimens, but usually between 4 and 7 mm. It is narrow, with apertural width rarely exceeding 1 mm. The stipes are 1 cm long and about 3 mm wide. The dorsal walls are essentially straight, although in some examples there is a gentle curvaturc. In better preserved specimens, the dorsal wall is undulate (Fig. 16j, 17j) due to the simple prothecal folding. Proximally the thecae are 5 mm long, distally they are up to 7 mm long. Inclination of thecae

decreases distally, e.g. $th6^1$ is inclined at 40° to the axis of the stipe while $th10^1$ is inclined at only 10° (specimen SM No. A 603142). Proximal thecae are strongly curved, distal thecae straight. Thecae number 10 in 10 mm, overlap 0.6. Denticles are pronounced. Apertural margins may be straight, concave or convex, are directed outwards in the proximal thecae, upwards in distal thecae.

REMARKS: This species has been discussed in detail by the author in a recent publication (Beavis 1972). Reference should be made to that paper.

***Pseudisograptus hastatus* (Harris)**

(Fig. 18a-g)

1914 *Didymograptus caduceus* var. *manubriatus* T. S. Hall

1933 *Isograptus hastatus* Harris

1972 *Pseudisograptus hastatus* Beavis

MATERIAL: Five specimens from Bagshot, near Bendigo, two specimens from the Castlemaine district, and three from Steiglitz.

HORIZON AND LOCALITIES: As Harris noted, the confusion with *P. manubriatus* has meant that many of the records are unreliable. It has a certain range from Ya1 to Da1. It has been collected from Yandoit, Castlemaine, Bagshot and Steiglitz.

DIAGNOSIS: Small rhabdosome of two stipes diverging at a small angle initially, but distally at 330° . Stipes

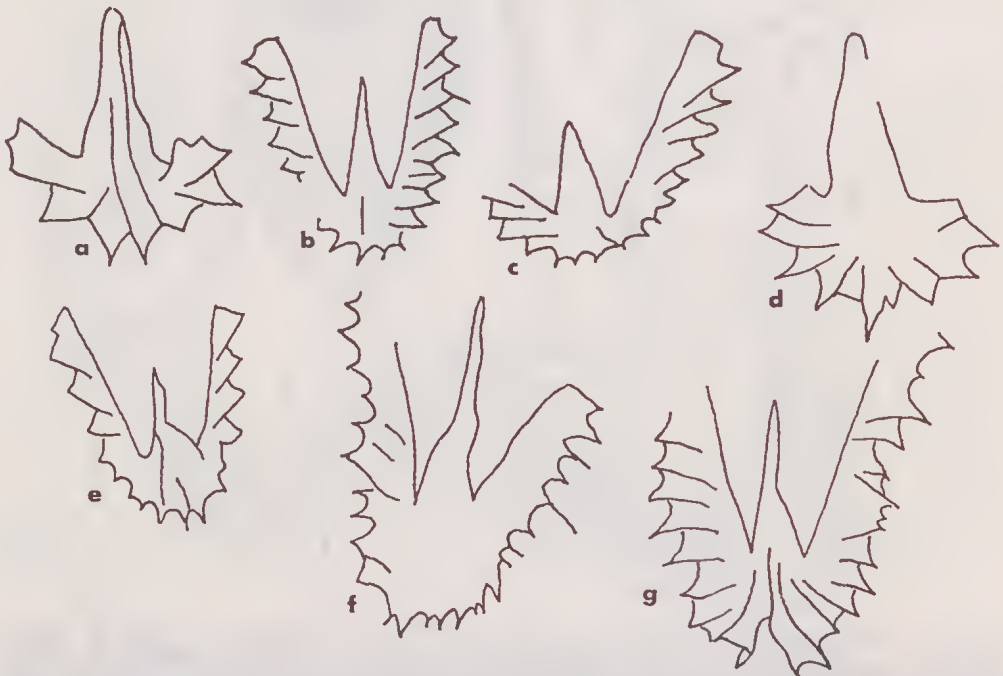


FIG. 18—*Pseudisograptus hastatus* (a) SM A6330 Juvenile form Limestone Ck, Yandoit, $\times 8$. (b) SM A6332a Sandy Creek Rd, Bagshot, $\times 4$. (c) SM A6332c Juvenile form, same locality as (b), $\times 8$. (d) SM A6332b Same locality as (b), $\times 4$. (e) SM A6331 McCrae Street, Castlemaine, $\times 4$. (f) GS 4098 Moorabool River, Steiglitz, $\times 4$. (g) GS 4099 Moorabool River, Steiglitz, $\times 4$.

taper gradually. Sicula long and tapering. Thecae simple tubes.

DESCRIPTION: The sicula is long (5 mm) and narrow (1.2 mm at the aperture), but appears to be broader. Initial thecae originate in the sicular region and have a *manubriatus* growth pattern. Thecae number 10 to 12 in 10 mm, overlap 0.45 to 0.6, are about 1 mm long and 0.4 to 0.5 mm wide. The denticle is prominent. Thecal apertures are concave and make an angle of up to 140° with the stipe axis.

The stipes are about 1 cm long and taper from a width of 0.7 mm proximally to 0.5 mm distally. Dorsal walls are straight.

REMARKS: T. S. Hall regarded this species as a variant of *P. manubriatus*; it is, however, quite a distinct form. The angle of divergence in *P. hastatus* is greater by some 30° and the thecae are smaller. The sicular region of the two forms is similar, but in *P. hastatus* the sicula itself is relatively longer and more sharply tapering, while, except for this, the initial thecae probably arise lower down in the area. The mode of proximal development appears to be the same in the two forms, essentially, but we cannot understand Harris' opinion that this anticipates the maeandrograptid type of development since *Maeandrograptus* appears first significantly earlier in the sequence than *Pseudisograptus*.

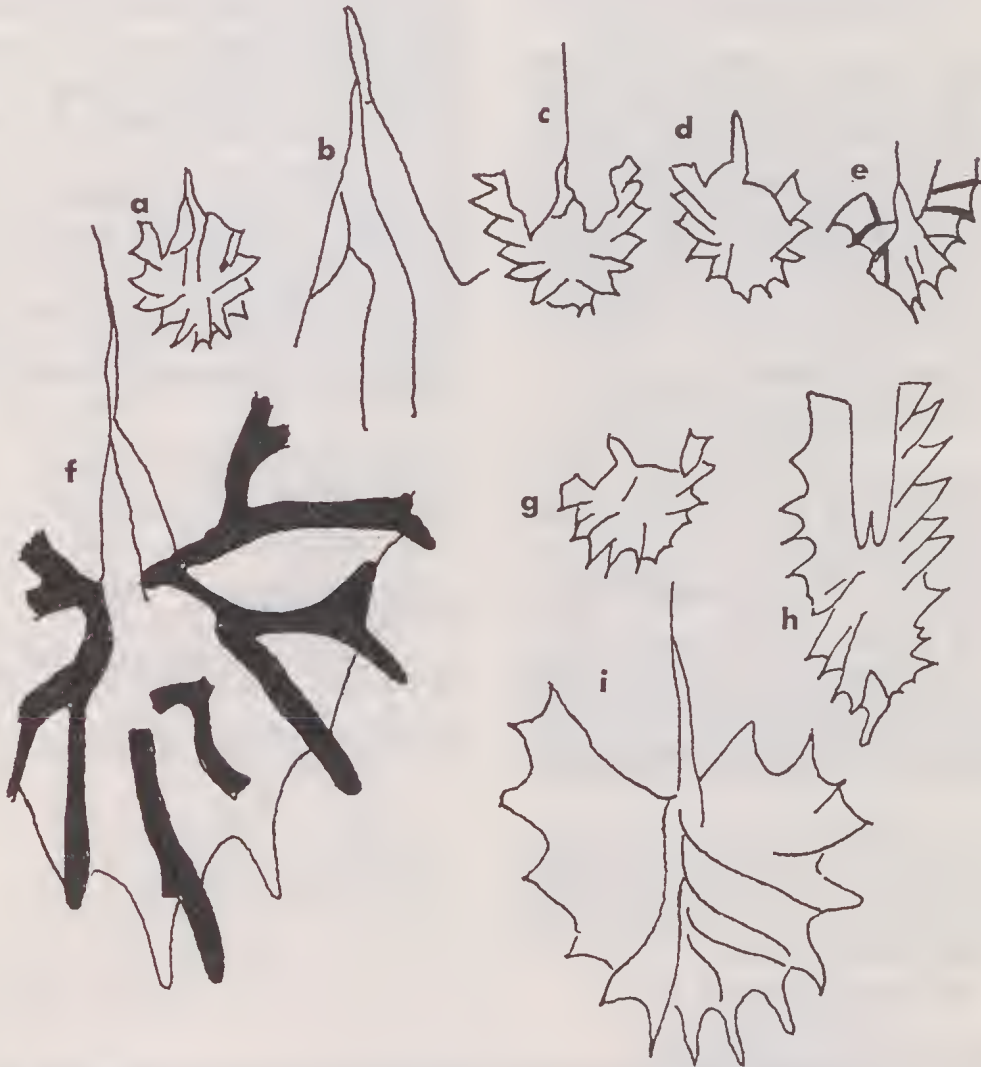


FIG. 19—*Pseudisograptus dumosus* (a) SM A22749 Locality Ba71, Gisborne, $\times 5$. (b) SM A22749 Sicular region, $\times 21$. (c) SM A6339 Lectotype, Loc. Ba71, Gisborne, $\times 5$. (d) SM A6340a Loc. Ba71, Gisborne, $\times 5$. (e) SM A6340b Loc. Ba71, Gisborne, $\times 5$. (f) SM A6340b Proximal region, $\times 21$. (g) SM A6336 Loc. Ba71, Gisborne, $\times 5$. (h) GS 5000 Moorabool River, Sheoaks, $\times 5$. (i) GS 5001 Little River, Brisbane Ranges, $\times 10$.

***Pseudisograptus dumosus* (Harris)**

(Fig. 19a-i)

1933 *Isograptus dumosus* Harris1972 *Pseudisograptus dumosus* Beavis

MATERIAL: Specimen SM No. A6339, locality Ba71 Gisborne is designated lectotype. Micaceous and carbonaceous film on white sandy siltstone. A further four examples from this locality were examined and figured. Several examples from Steiglitz, poorly preserved.

HORIZON AND LOCALITIES: Restricted to Yapeenian Ya1 and Ya2. Recorded from Gisborne, Yandoit, Castlemaine, Muckleford and Steiglitz.

DIAGNOSIS: Rhabdosome small; stipes diverge initially at 310° but this increases sharply to 360° . Thecae curved.

DESCRIPTION: The sicula is long and apparently slender: length varies, but averages 3 mm. The apparently broad sicular region is due to the concentration of thecal origins in this region. The stipes are 4 mm long and 1 mm or slightly less wide, although one example (SM No. A6340b) has stipes almost 8 mm long. Thecae number 8 to 9 in 10 mm, overlap 0.7 to 0.95, decreasing distally. The thecae are curved, 1.5 mm long, 0.4 mm wide. Apertural margins may be straight, concave or convex, and are directed upwards, except in the proximal thecae, in which they are directed outwards.

Genus *Maeandrograptus* Moberg 1892***Maeandrograptus tau* Harris**

(Fig. 20a-b)

1933 *Maeandrograptus tau* n. sp. Harris

MATERIAL: The holotype (NV No. 13798) and two other specimens from Gisborne.

HORIZON AND LOCALITIES: Known from Gisborne and Macedon. Probable range Castlemanian Ca3 to Yapeenian Ya1.

DESCRIPTION: Small rhabdosome of two stipes each less than 5 mm diverging at 180° or slightly more. The sicula is long: 5 to 6 mm. Thecae are sharply inclined, 1.5 mm long, and 0.4 to 0.5 mm wide. Ventral margins sigmoidally curved, apertural margins concave. Thecae number 9 in 10 mm. Overlap 0.35 to 0.5.

REMARKS: Harris referred this species to *Maeandrograptus* because of the nature of the sicular region and because the thecae are typically maeandrograptid. While stipes of only 3 or 4 thecae are most typical, examples with stipes up to 1 cm long have been found at Wileys Quarry, Macedon.

***Maeandrograptus aggestus* Harris**

(Fig. 20c, d)

1933 *Maeandrograptus aggestus* Harris

MATERIAL: The only existing specimens: the type specimens NV No. 13799, Yandoit, Victoria.

HORIZON AND LOCALITIES: Known only from Ca3-Ya1 transition beds, Yandoit.

DESCRIPTION: Rhabdosome small, triangular, the shape resulting from the grouping of the thecal origins in the sicular region. The early thecae grow downwards, turning outwards in the apertural region; later thecae grow entirely outwards. Thecae are long tubes (1.2 mm) and narrow (0.3 mm), early thecal overlap is 0.5, in later thecae, overlap is 1.0. Apertures slightly concave.

CONCLUSIONS

On morphological evidence, the family Isograptidae Harris 1933 has been reduced in status to the sub-familial level. The sub-family Isograptinae includes the single genus *Isograptus*. The genera *Oncograptus* and *Cardiograptus* have been transferred to the sub-family Cardiograptinae Mu and Zhan, *Maeandrograptus* and the 'manubriate isograptids' i.e. *Pseudisograptus* have been transferred to the family Sinograptidae Mu 1957. *Skiagraptus* is tentatively regarded as a dichograptid.

It is considered that *Isograptus victoriae* and *Isograptus gibberulus* are probably conspecific. The varieties of *I. caduceus* figured by Harris have been raised to specific status. The evolutionary trends postulated by Harris have been modified so that while the trend: *I. Primulus* → *I. lunatus* → *I. victoriae* → *I. maximus* → *I. maximo-divergens* → *I. divergens* has been substantiated,

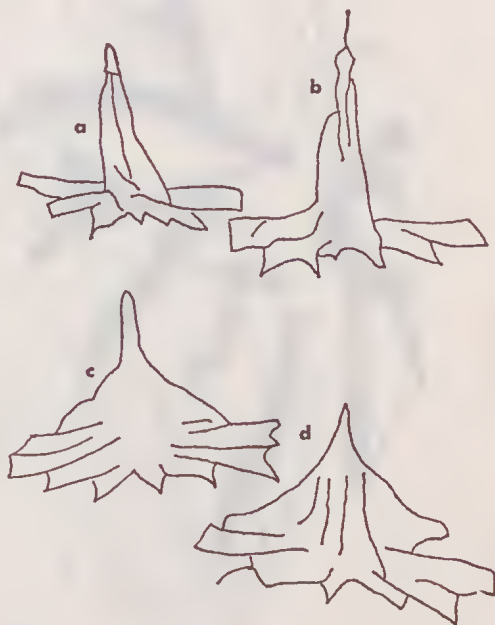


FIG. 20—*Maeandrograptus tau* (a) SM A6334 Loc. Ba71, Gisborne, $\times 6$. (b) SM A6335 Loc. Ba71, Gisborne, $\times 6$. *Maeandrograptus aggestus* (c) NV 13799a, Holotype, Allot. 2, Sect. 2, Yandoit, $\times 9$. (d) NV 13799b Same locality as (c), $\times 9$.

most of the other postulated trends have proved to be invalid on either or both palaeontological and stratigraphic evidence.

The genus *Pseudisograptus* has almost certainly developed from *Maendrograptus*, and *Cardiograptus* is clearly descended from *Oncograptus*, but the ancestries of *Oncograptus* and of *Skia-graptus* are uncertain.

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DESIGN AND THE LIVING ENVIRONMENT

By D. G. D. YENCKEN*

Paper delivered at the Royal Society Symposium 'The Urban Environment and Life', September 13, 1973

Design is an emotive word. To the systems or production engineer it means practical planning; to many architects visual quality, the lifeblood of all values; to many of the architects' clients, what architects do—'at our expense'. Architectural critics have sought to isolate universal qualities in the great design of all ages, but it is an elusive search in which different cultural perspectives play odd tricks on our attitudes and judgements.

Just such an architectural critic mindful of his duty to protect his cultural tradition wrote in an obituary on Nash (the Nash we now revere as the Great Architect of Georgian England):

Died at his seat, East Cowes, Isle of Wight, in his 83rd year, John Nash, esq. As a speculative builder, this gentleman amassed a large fortune; but as an architect, he did not achieve any thing that will confer upon him lasting reputation, although he certainly had frequent and first-rate opportunities of doing so. The new palace in St. James's-park, has certainly added nothing to his fame in any respect, for it is universally admitted to be a most signal monument of extravagance and meanness combined—to be altogether a complete failure as a piece of architecture. Mr. Nash seems to have possessed neither grandeur in his general conception, nor any taste in his details, which look as if hurriedly sketched out, and never finished . . . *Annual Register*, 1835.

Perhaps this is above all an example of the emotion generated by amassing large fortunes. However, if architects cannot agree about architectural qualities until at least a century has put those qualities in some kind of cultural perspective, it is clear that there cannot be any single definitive design style which is applicable today to the whole area of housing and residential planning. This is now much better understood by most people involved in residential decision making. There is an increasing awareness of the extraordinary diversity of reactions which people of different cultural backgrounds, upbringings, interests and

psychological make-up may bring to different environments; of the costs attached to unsatisfactory environments, costs related to direct inefficiencies, and psychic costs, instability, stress and so on.

The need to identify and to measure individual and group requirements is therefore now beginning to be accepted as an essential pre-requisite to the design of a satisfactory living environment. This paper is concerned with how this diversity of environmental reaction can be identified and with some of the ways different users' requirements can be most satisfactorily met.

* * *

Firstly the extraordinary range of environmental influences makes adequate identification of real needs very difficult. Even when this identification research work is professionally carried out there is no certainty of complete success. Although the professional should have a grasp of the complexity of influences and the importance of different cultural traditions, and although his techniques of measurement should also be less liable to distortion and bias, he is as liable to general error and as liable to be influenced by current fashion in his profession as any other investigator. When the professional is working with people of different social and economic status—very low income families, people of different nationalities, aborigines—the problems are further compounded. There are many well documented professional misadventures in these areas.

The identification of cultural patterns and basic needs related to those patterns can therefore be a very difficult and sensitive problem. At different times through the paper I will refer to these problems again. However, given these very great difficulties, it is possible to state two important principles for the design of any living environment. The first principle is that the greatest range

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of environmental choice should be available in the society. The second is that within that wide range the greatest opportunity for personal selection and self expression should be available to all members of the society. I am of course talking about a complex diverse society such as our own and not about a primitive homogeneous society.

The importance of freedom of choice is underlined by research evidence that both animals and man in natural conditions firstly select their habitat and secondly modify it after they have selected it; and that animals as well as man exhibit signs of stress when they are unable to select and modify.

There is further evidence that the human stress of adaptation to a strange environment can be greatly reduced if the individual has some involvement in the initial choice and some control over the later development and functioning of this new environment. The way in which this variety of opportunities can be achieved and the freedom of the individual to choose within these opportunities are therefore of very great importance to the society.

* * *

The complexity of the planning process firstly demands the involvement of a variety of skills. The organization and relationship of these skills is in turn a matter of fine adjustment. A good example of the process might be that of the changing role of the architect in planning. Recently there has been a significant reaction against visual, architectural planning. There have been good grounds for this reaction. However, it is unfair to say that the architect has been the primary cause of the problem. A better appreciation has led to the understanding that it is the system which has been wrong and not the individual performer, that it is not the architect's fault that he has quite unreasonably been asked to be a *Uomo Universale*. This has led to the development of more and more team approaches to design, where trained analysts, economists, sociologists and so on are asked to identify general forces and individual needs and then to write a comprehensive brief before the architect is asked to respond to it, and where all the experts participate in the final selection. However, in this group process the designer still has an extremely important part. The point is that there are different roles required in a team effort, not just managerial and specialist but also analytic and synthesizing.

I am not trying to give you a treatise on organization. However, the successes and failures of complex planning problems so much depend on

the process, and the importance of the process is often so poorly understood, that any discussion on design and its effect on living environments has to deal with these issues. The possibilities and difficulties of public participation in planning decision-making illustrate this point nicely. It is now a planning act of faith to believe in the principle of public participation. But to believe in the principle is one thing and to carry it out effectively is quite another. The public just may not want to participate. Some people may believe they have better things to do like playing golf, shooting craps or drinking beer. This will not, however, stop them from bitterly criticizing the plan and the planners if, later, when the plan starts to affect their lives, they do not like it. In turn the professionals who do want to participate will not necessarily participate in the way the planners have proposed. There are also competing demands on their time and interests.

A planning process based on the assumption that people will act in an orderly logical way is a poor process and unlikely to succeed. The process has therefore to encompass and provide for the irrational, and the planning methodology has to be much more subtle and responsive than is normally understood.

However, it is not enough to assume that a good solution will automatically develop from a well considered planning approach. Any technique will almost certainly have important limitations. The exercise is usually not a continuing but a finite exercise, probably completed with an enormous sigh of relief. There may be major deficiencies no matter how well it is carried through, due to reasonable mistakes of interpretation, lack of time for adequate research and a host of other reasons. So apart from having and using a good technique for solving the initial problems there has to be also a means of continuous adjustment to people's needs and preferences. How can this happen?

* * *

In the private sector the market place is the well known mechanism for expression of personal preference. There is no doubt that the market place is indeed a very real corrective to misconception of need or appropriateness or satisfaction. When my partner and I started Merchant Builders we, and our architect, worked over our initial plans for many, many hours and revised them many times. Our first two or three clients very quickly disposed of any ideas we had that the plans were readily adaptable to different site conditions and client requirements. It is quite

extraordinarily difficult to plan very effectively for a great diversity of people and situations. The market place is continuously reminding planners, architects and builders of this fact, often very painfully.

However, the market place has its well known deficiencies too. It works well for the affluent, often not at all for the very poor. It is a part of a system which encourages materialist and consumer values, with perhaps a preoccupation with status and glamour. Not the least of its limitations is that it is also subject to controls which limit its opportunity to provide a better flow of innovative alternatives. The controls, the rules established by the State to regulate planning, house design and construction are themselves a product of the system. All developed in some sense as correctives to the unfettered freedom of action of 'unscrupulous profit seekers' in private industry.

The developer's stereotype is well understood. 'You do everything you legally can to exploit all the opportunities within the rules to maximize your profit.' However, in return the rule makers and rule operators have their own stereotypes: innate suspicion of any proposal for change on the assumption that either the proposer is himself seeking some carefully veiled advantage which will not appear until the scheme has been approved and built, or alternatively that there will be established a precedent which will be systematically exploited by all the other 'baddies' in ways which cannot be clearly foreseen but are nonetheless real. These descriptions, in which of course there is some truth, are at the same time gross over-simplifications. People rarely behave entirely consistently; motives vary enormously between different individuals within the system and indeed between different individuals in the same organization. The result therefore all too often seems to be a confrontation, not a dialectic. Rule making which actively sets out to make change and experimentation possible under controlled conditions rather than rule making which sets out only to put curbs and chains on private activity is an essential need. I shall have a little more to say about this later.

In public housing areas the issues are different. The public housing authorities in fact came into existence precisely in order to overcome the problems inherent in the market system. Most but not all of these market system problems are therefore not of major significance in the public area. The public housing authorities have considerable freedom from the regulatory constraints imposed on the private sector or, if not, at least a better bargaining power. There are, however,

other rules related to their charters and the Housing Agreements which do put real restraints on them. Nonetheless, a determined Minister and a determined authority could quickly vary or adapt these rules.

What the housing authority does not have is any built-in system to determine user preference. The user has to take the very limited range of choices offered because he has no other alternatives. The organizations are large organizations, the problems are problems of logistics, long waiting lists, available resources, maximum production in the shortest time within the scope offered by the resources. It is no wonder that the authorities are production orientated, run by production minded people. The problem is that though total concentration of effort on the production process may often indeed result in efficient production, the product may be quite inappropriate. It may not answer real needs or provide the freedom of choice it could, and may even under certain circumstances be producing worse conditions than the conditions it replaces, at great cost to the total community.

How is it possible to introduce greater respect for user needs and preferences? One way is to improve the planning process by bringing in sociologists and other professionals, by using better planning procedures, and by other public participation exercises. But this process has also all the defects I have described. The planning will be done by the professionals, a wider range of professionals to be sure, and using methods, good methods, to create good interactions among the professionals, but it is likely to be an exercise by the professionals only and very often fails to involve the users themselves. The users in public authority housing are poor, come from different backgrounds from the professionals, feel insecure with them, are unaccustomed to dealing in concepts or reading plans, and are usually unable or unwilling to be interested in the process. The planners are still in that unhappy situation of planning for other people and particularly planning for other people of entirely different backgrounds and cultural values.

Really sensitive answers which are truly responsive to the needs of the users are difficult to achieve by these methods, especially when the process is a continuous process. The more the planners and designers go through their exercise the more they tend to become fixed in their attitudes, the less receptive to new information and ideas. It is a human characteristic.

There are therefore serious limitations to paternalistic planning. In the United States, partly

in response to these problems, partly in order to tap the resources of private industry, a whole range of housing programs have been instituted over the last ten years or so. (Most have now been dropped by the Nixon administration along with other welfare programs.) The programs, which were many and various, sought primarily to use private industry to provide low income housing by interest subsidy, turnkey operation (undertakings to purchase schemes built by private enterprise at the time of their completion), and other such devices. There were real successes with these programs, successes related to cheaper construction and a wider range of housing types and therefore some extended choice. Unfortunately many of the successes were overshadowed by scandals of graft and misappropriation. The programs also failed to provide for the really poor. Although a series of presidential advisory committees has drawn attention to these deficiencies most of their recommendations have not been put into effect.

Despite their aura of failure these programs deserve serious consideration in Australia. As so often happens when something does not work, the concept is blamed when very often the concept may be quite satisfactory but the technique used to carry it out inadequate. The particular merit of these housing programs, leaving aside the cost reductions reported in the advisory committees' findings, was to open up a wider variety of housing opportunities by providing a little more of the freedom of choice to be found in the more affluent private housing market.

The programs have, however, many limitations. In them there still remains a very large element of paternalism. As a reaction to these limitations a new movement in the U.S. has produced some interesting new ideas for the further extension of opportunities for the low income earner to make his own housing choice. In a book called *Freedom to Build*, John Turner and a group of architects and other professionals—some who have worked on housing programs in the developing countries, some who have been concerned with housing in the United States—have drawn attention to the fact that a huge neglected area of the housing market is the market of self-built housing, houses ranging from those built wholly by the owner's labour, to houses largely subcontracted under the owner's direction. The authors point out that in the U.S., despite its affluence and its technology and despite the size and power of its large corporations, still over 15% of the total housing completions are owner built. What is more important is that the houses are built for

about 60% of the ordinary cost of a house and are built the way the owner wants them. For the owner there is the dignifying benefit of making his own decisions. He has to learn to deal with the authorities and may therefore also find a new confidence moving about in a foreign organizational world. Finally involvement in the building process means a very different attitude to the house when it is built. This is particularly important when the technique is applied to rental housing, i.e. when occupiers renovate their housing. The change in maintenance costs in this situation can be dramatic. This large market, it should be remembered, also exists without the benefit of ordinary housing loans which are not normally available to the owner-builder in quite the same form, if at all.

In Australia there is an equally substantial and equally forgotten segment of the housing market occupied by the owner-builders. In the year ending 72/73 there were 13,495 completions of owner built houses, 12.9% of the total number of private completions for the year. Furthermore there were in the same year 16,018 commencements of owner built houses, 13.4% of the total private commencements for the year. The numbers of owner-builders therefore seems to be growing, not declining. If this group already exists in such numbers, unrecognized and unassisted, what might not be possible if Governments concentrated on servicing potential owner-builders as an alternative to providing predetermined housing at infinitely higher cost. Such a process allied to income subsidies might also have a really dramatic effect on the housing authorities; a truly Marxist possibility of the withering away of the State!

Other extensions of this idea have fascinating possibilities. The role of the professional, the architect for example, might change from being that of design determiner to that of adviser and counsellor, teaching environmental consciousness and appreciation of basic design as well as assisting in more practical ways, working by suggestion and example rather than by decree. The role would be a much more subtle and difficult one but also a much more rewarding one, however imperfectly accomplished, because the process would be an involving and learning process for all the parties. The possibilities extend further into the creation of communities. This is not just a fanciful notion. In the U.S. there are already some remarkable examples of community design projects carried out in just this way.

Owner-building is one entirely practical alternative to the existing methods of producing low

MANNINGHAM RD.

15' HIGH

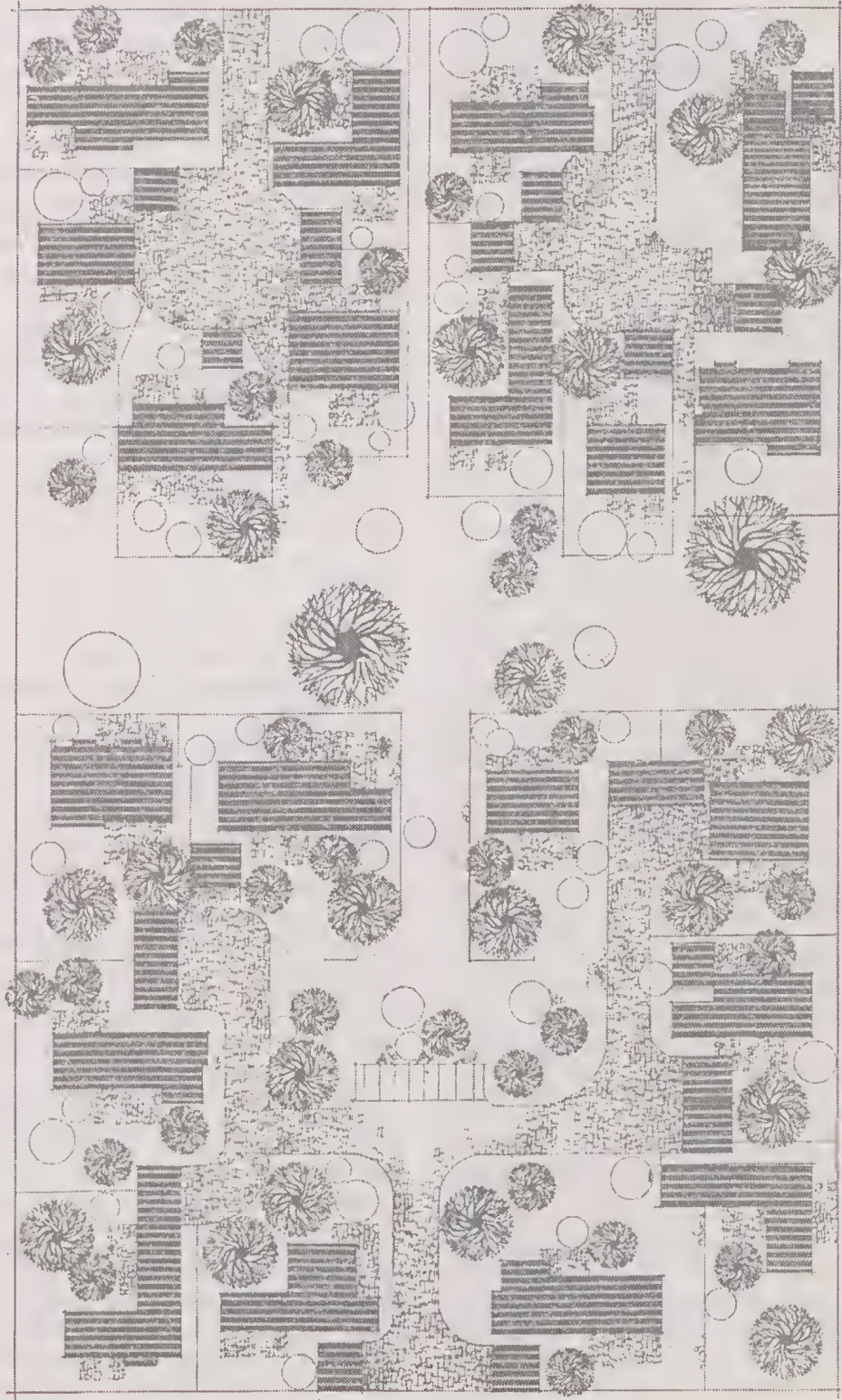


Fig. 1—Winter Park, Doncaster, Victoria: Layout of cluster plan. 20 houses on 4.3 acres.

income housing, an alternative which can be accomplished at very much reduced cost to the community and much greater satisfaction to the householder. There would of course continue to be a need for housing supplied by more conventional methods since owner building would not suit all requirements. It is, however, providing the alternatives which is important.

Let me now return to the private sector. I have mentioned that the main obstructions to greater innovation and thus variety and alternative choice are the obstructions of regulations and the manner in which these regulations are interpreted. This needs emphasizing and re-emphasizing because there is a very commonly held belief, both a popular belief and a professional belief, that our society is indifferent toward new ideas and the possible benefits of these new ideas. The popular expression is seen through the writings of the pundits on the Australian way of life. It is seen amongst sociologists, particularly perhaps those sociologists indignant about the growth of consumer values and the way these consumer values have affected life styles. Some are so conscious of the flagrant marketing techniques used in housing developments that they overlook the very real improvement in house planning which has taken place over the years. There are I believe special reasons why intellectuals, especially social critics, hold these views and why it is important that they should continue to present them. However, my experience is contrary to this thesis. If a new idea can be put into practice there is always a small group ready and willing to adopt it, for whatever motive, provided that the necessary conditions of time, place and relative cost are adequately met—that is, the conditions related to good management and good judgement.

I could give you many examples of misjudgements about interesting new ideas, but I prefer to give you an example of the successful execution of a novel concept because I think it makes the point better. Some two years ago my company started a small development of freely sited houses in Doncaster. The principle behind the cluster idea was to plan the development to respond to the natural features of the site, sun, slope, trees, views, and to site the houses in the most sensible relationship to each other. As the illustrations, Fig. 1 and Pl. 12 show, the effect is very different from a conventional subdivision although the density of development was not changed. In the cluster group there are some further signal benefits. Although each house has its own private garden, well related to the living areas of the house, rational planning has reserved nearly 25%

of the site for common open space. This common open space in turn allows the possibility of interesting new social interactions. There are many other points I could make about the scheme. However, it is the changes in reaction over the various stages of the development—from the time the idea was first proposed through its early development up to its completed operating finished form—which are most interesting. Although residents' changing reactions to the sharing of communal land and facilities is an intriguing social study in itself, it is the authorities' change in attitude which is really startling. Before the scheme began and even in its early days it had relatively few advocates. Now municipal officers speak eagerly of the potentialities of cluster development. Legislation to facilitate cluster development is likely to be introduced within a few months, and, looking forward a few years, it is not fanciful to consider that a large part of Melbourne's future development may be carried out in cluster form. This is an illustration of the power of example, of the force of a new idea when that new idea can be put into a physical form. It is, however, difficult and expensive for private enterprise to carry out these experiments in the present climate of bureaucratic thinking. Other alternatives are needed.

I have mentioned the fear of setting precedent which seems to be the all pervasive fear which paralyses intelligent response from authorities. Somehow authorities must be taught to look for improvements and innovation and to be ready to assist their progress. Since, however, mere exhortation is not likely to change these attitudes very greatly or very quickly, it seems that other devices are necessary. Some of these devices include provisions in all planning schemes for comprehensive planning proposals which do not necessarily comply with existing regulations and the opportunity to submit to a superior authority or appeal body which would have powers to waive those regulations, proposals which can be seen to be in the public interest.

Most important of all would be any active steps which Government can take to change the emphasis towards innovation and experimentation. The most effective way of achieving such a change of emphasis would seem to be to create machinery for social experiments. The machinery must involve ideas which can be collected from the whole community, not just the ideas which are generated within a bureaucratic institution, public or private. One way this might be done is through a special experimental program. Governments might for example invite submissions for

social experiments from the whole community. They would then evaluate these submissions, select a few for development, provide support either by underwriting or through low interest loans, make possible the very quick passage of permit application (if necessary by waiving existing regulations, normally a problem of great importance with applications for innovative developments) and finally provide the means for very careful measurement of the successes and failures of the experiment.

The advantage of such a process is not merely to draw on the community's ideas, but also to find means of carrying out and measuring controlled experiments with those ideas. It is also to emphasize that Government action should be positively as well as negatively directed, to foster the good as much as to prevent the bad.

This is a process which has equal benefit to both

public and private sectors. It is also a research experiment process which would run parallel to experimental projects public authorities should be carrying out in their own right.

All of these ideas are ideas aimed at providing answers which satisfy the two basic principles set out at the beginning of this paper: firstly a wider range of housing opportunities, and secondly greater opportunity for individual choice and self expression within those opportunities.

In seeking to provide these answers, it is important to remember that the distinctions between public and private action are in themselves distinctions of little importance. The differences are in any case now differences of degree only. What is important is to provide the best answer within the total resources which are available to the community and to use those resources to the greatest possible advantage.

DESCRIPTION OF PLATE 12

Winter Park, Doncaster, Victoria: View of four houses and a part of the communal open space.



LAW AND ECONOMICS

By GEORGE A. KAUFMANN*

*Paper delivered at the Royal Society Symposium 'The Urban Environment and Life', September 13, 1973**Tempora mutantur nos et mutantur in illis.*

People are selfish, law givers corrupt and the citizen in despair. Thus appears the world in our day. In this paper I discuss our arrangements for living together and preserving at least some of the more pleasant things for our children.

I take it that individuals will maximize their satisfactions by accumulating as many assets and resources as possible, reducing the ability of others to do so . . . that people will not deliberately foul their environment, but will not go to very much trouble to improve it unless they profit in some way . . . that views on desirable habitats differ between age groups, social classes, local groups, and over periods of time.

The results are conflict and contradictions. These may be resolved by the planning of all activities, directing all people in accordance with these plans; by allowing physical, mental and economic power to determine possession and enjoyment of resources; or by some consensus on the degree of planning and restraint of free enterprise.

I cannot review the noble ideas proposed by generations of philosophers and political scientists to lead mankind to terrestrial happiness or at least to immortal rewards. I can only note that none have secured the promised happiness of all mankind. This will not, of course, deter future philosophers from fashioning more plausible ideologies equally unlikely to solve the predicament of man.

Instead, I shall examine the state of affairs in contemporary Victoria, seeking to identify the social, economic and legal powers which contribute to the present distribution and enjoyment of resources, and venture some predictions on their composition during the next two or three decades.

Most productive resources are owned by individuals or groups who use them to further their

own interests, mainly to enlarge them and to make profits. These people reject direction and interference by the community or the State, claiming that their unfettered activities will lead to the most economic deployment of the scarce resources. Such entrepreneurial groups would also assert that profits will reward those who serve a genuine demand. This, in turn, will ensure sufficient and stable employment for those who do not command capital.

Urban land, used for housing rather than productivity, is owned by a multitude of house owners, land lords and the public authorities. Land for public services, roads, enjoyment and recreation is predominantly vested in local or State authorities. Until fairly recently, it was generally held that buying and selling of privately owned assets, whether productive or domestic, should be unrestrained. Supply and demand would determine price and, apart from short term fluctuations, equilibrium would prevail. As a concomitant, save for the broadest considerations of communal health and safety, anyone should be able to use his property as he thought fit. The desire to impress, and the condemnation of the neighbours, were thought to ensure reasonable standards of construction and care.

The provision of those services which needed resources beyond the capacity of the individual was delegated to co-operatives, local and State authorities. These services were funded through rates and taxes which were preferably designated according to their specific purposes. Users were meant to defray the cost of operation. The care of the poor was left to private charity, the protection of private property was the care of the State and its insurance of the owners.

Lately, however, things are changing. Industrial progress and development have led to explosive growth of the metropolis and some country

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towns. Real incomes have increased and led to general affluence. The number of entrepreneurs has declined; the wage earner is found in occupations previously followed largely as self-employment. Inequalities in assets and earnings, though not greater than before, are resented, and a general egalitarian norm is sought more widely. Workers rely on their employers to arrange their tasks, direct them in their execution and provide plant and amenities alike. This mentality has now spread to people's thoughts on how their domestic affairs should be arranged. They want to be told where they should live, what their houses are to be like, how they are to be financed; they look for somebody to provide water, gas, electricity, sewerage, schools, health services, age care and transport. Individual enterprise is demcaned, the welfare state glorified.

This then, I believe, is the position we have reached: most people want to have their lives determined for them, their amenities supplied, and the education of their children, as well as health care and care in old age provided by a benevolent authority. If this be granted, bureaucracy, planning and restrictive legislation follow.

This leads, inevitably, to the setting of standards, e.g. in education, housing, medical care, etc., by theoretical experts who know what is good for others, but rarely either what they themselves or the people they plan for need or want. It leads to interminable research into the goodness and 'socio-politico-economic' status of the expert solutions, to facility for the initiated, adventurous and ruthless to manipulate supply and demand in resources likely to be encompassed in planning schemes. It brings about the emergence of verbally fluent individuals and groups who question the standards set, not in relation to the needs of the multitude, but by some aesthetic intellectual cerebration, and a pervasive attitude that a mysterious community will provide greater benefits than each puts into the common fund.

The contradictions amongst people created by their dependency complexes and their greed and individual aspirations, by their wish to benefit more from their membership of the community than the amount of their contribution to it, could lead to violence and sociological upset, unless very detailed regulations and ordinances prescribe communal interactions.

Until lately, the most potent laws ensured the possession and enjoyment of assets, independently of their mode of acquisition or the inconvenience imposed on others in their use. We now perceive a subtle change. Use and enjoyment of private property are restrained by the expertly set stan-

dards purporting to reflect the common good. Industry, commerce, high and low density housing are assigned their separate zones, local governments prescribe whether these buildings be stone, brick or timber, how far they have to be from footpaths and boundaries, whether they be permitted sheds, garages and swimming pools, and ensure that their design does not offend the surrounding uniformity. The authority of the local council is upheld and subjugated to the metropolitan planning authority and, ultimately, to the State and Commonwealth governments who try to provide grand strategies and frameworks within which the individual citizen can unfold his life in the stream of general progress towards equality and prosperity. The feasibility of this grand design is rarely questioned.

It is held axiomatically that individual action and decisions in our complex technological society must lead to deterioration of the environment, to restraint of healthy survival and to the lessening of vital enjoyment. Direction is, therefore, necessary. I could agree that almost any activity produces some pollution, insignificant in each instance, but cumulatively dangerous to the health of the community. The cost of reducing smoke, poisonous effluents, fumes, debris is seldom of benefit to the polluter. He is often unaware of their cumulative effects. Therefore, he will not do anything to remedy his offence unless he is forced to or is persuaded of his obligation by heightened awareness. We seem to have favoured legal regulation with its need for licensing and an army of inspectors. Evasion, pretence and even collusive bribery must result. Perhaps greater awareness could be achieved through education and example, leading to co-operation rather than compliance.

Poor sanitation, contaminated food, physical inactivity and abuse of alcohol and drugs tend to lower health and vitality of people. It is assumed that people generally will neglect their health unless they be forced to look after themselves. Once again, we rely on legislative direction rather than the provision of information and knowledge which would enthruse people to do for themselves what benefits them. Thus we have compulsory chest X-rays, fluoridation of water supply proposals, and an ambivalent attitude to advertising harmful substances. We carefully preserve the human body to an old age in which the will to live bows before the spare-part surgery and the artificial extension of living death.

Conurbation removes the ordinary citizen from the real food producer and interposes a chain of middlemen for the provision of the

necessities of daily life. The consumer's choice and appreciation of the goods offered declines in the supermarket economy. He is prone to exploitation and many opportunities for deceit and profitmaking arise. We respond by legislative direction. We have an elaborate set of food and drug regulations which specify additives according to their ability to produce cancers in carefully bred and selected rats. We prescribe the printing points of labels and set out the information to be conveyed. But nothing really serious is done to inform the consumer of the meaning and import of the protection afforded to him. Therefore, the manufacturer incurs the cost of complying with the multiplicity of regulations, duly passes it on to his customer, but seldom ensures that the intention of the law, the enlightenment of the consumer, is achieved.

In many other fields also, the scientist, sociologist, planner and the philosopher have persuaded the law giver, and often the citizen, that the natural instinct and enterprise of the individual are defective and that the sum of all happiness

is increased by reducing individual satisfactions.

Hence, it is no illusion if we see ourselves hedged in by a multitude of laws and ordinances designed to achieve some academic and often quite impractical social and economic design. Our frustration turns to impotent fury when we see the clever, knowing and well-established, take advantage of these very restraints and, manipulating and circumventing the procedures open to all, appropriate to themselves an undue share of assets and resources.

What then of the future? If we believe man to be intelligent, we should not impede his evolution with restrictions, commandments, ordinances and prescriptions. We should show instead, by example, how despicable greed, arrogance and the suppression of others, in the name of spurious law and order, really are. We should, thus, reinforce the attempts of young men and women everywhere to grow into free people, making their own judgements and being happy in the fulfilment of personal dignity. To do this, our lawgivers must abolish the worst legislative restraints and governmental direction of our lives.

ENVIRONMENTAL DESIGN OF URBAN AREAS

By BARRY McNEILL*

Paper delivered at the Royal Society Symposium 'The Urban Environment and Life', September 13, 1973

ABSTRACT: Contrary to conventional belief our large cities have generally improved their quality over the past half century. The main physical problems are associated with air quality, transportation and the excessive spatial segregation of socio-economic groups usually to the disadvantage of the poor. But the planning and management of urban areas is the most important problem we are facing. There are relatively simple physical design approaches that could improve public transport, opportunities and the environmental quality of both living and working areas, but the key solutions lie in the reform of urban government and the creation of socio-political opportunities for lower socio-economic groups.

The word environment is widely used in the current upsurge of community awareness. I prefer to define environment in Buckminster Fuller's sense of 'everything that isn't you'. But perhaps I also should define environmental design. This is a general term used to describe those professions which intervene in the environment: i.e. design, architecture, planning and even civil engineering.

The term has come to be used to emphasize:

1. An appreciation of the complexity of the environment and the interdependence of all its elements, including man.
2. A problem-solving orientation rather than a solution emphasis.
3. An appreciation of long term community goals rather than short term sectional material gain.

But in historical sense this approach is of course not new. In 1902 Ebenezer Howard introduced the chapter on Administration in *Garden Cities of Tomorrow* by quoting from Albert Shaw's *Municipal Government in Great Britain* published in 1895¹:

The present evils of city life are temporary and remediable. The abolition of the slums, and the destruction of their virus, are as feasible as the

drainage of a swamp, and the total dissipation of its miasmas. The conditions and circumstances that surround the lives of the masses of the people in modern cities can be so adjusted to their needs as to result in the highest development of the race, in body, in mind and in moral character. The so-called problems of the modern city are but the various phases of the one main question. How can the environment be most perfectly adapted to the welfare of urban populations? And science can meet and answer every one of these problems. The science of the modern city—of the ordering of the common concerns in dense population groups—draws upon many branches of theoretical and practical knowledge. It includes administrative science, statistical science, engineering and technological science, sanitary science, and educational social and moral science. If one uses the term City Government in the large sense that makes it inclusive of this entire ordering of the general affairs and interests of the community, and, further, if one grasps the idea that the cheerful and rational acceptance of urban life as a great social fact demands that the City Government should proceed to make such urban life conduce positively to the welfare of all the people whose lawful interests bring them together as denizens of great towns, he will understand the point of view from which this book has been written.

It is obvious to all of us that the concept of interdisciplinary urban government and planning is, even at this point some 80 years later, still on the horizon. But it is still important to reflect on the current urban condition and provide a general

¹ Shaw, A. *Municipal Government in Great Britain* 1895. Quoted by Howard, E. in *Garden Cities of Tomorrow* (edited by F. J. Osborn), Cambridge, Mass. M.I.T. Press 1965, p. 89.

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analysis against which one can pose courses for action.

Contrary to conventional thinking, our large cities have generally improved their quality over the past half century. It is important to remember this, since there is a great tradition amongst western intellectuals, especially in the English-speaking world, to take romantic and irrational attitudes toward the city.² This is particularly true of many from the physical sciences. In recent times it is mainly the social sciences which provide penetrating analyses of the urban condition.

Let us briefly consider some of the myths of anti-urbanism³:

1. *Big cities are inefficient.* All empirical evidence suggests the contrary. Simply speaking, the larger the city the more economically efficient it is. Even New York does not seem to have reached any optimum size where marginal product is equal to or less than marginal cost.

2. *Big cities are uneconomical to service.* Although there are trade-offs between density, standard of living, technology and geographical factors, generally speaking empirical studies show the contrary.

3. *Big cities show extreme social pathologies.* Again, generalizing, this is not so. Social pathologies are related to social factors rather than size *per se*.

4. *High densities show extreme social pathologies.* Acceptable living densities are related to cultural variables and there is no direct relationship.

But there are some deteriorating indices in urban living. Air quality, at least in warm-climate cities where domestic heating by poor coal was not traditional, has deteriorated due to industrialization, but especially due to the use of the internal combustion engine to power our current form of personal ground vehicle. Public transport

is in difficulties, again largely due to the same ground vehicle. More importantly perhaps, and more especially so in recent times, the spatial organization of the city has developed disadvantages to the poor, often as a result of so-called 'social measures' such as 'slum clearance' and 'public housing'.

There are two main ways in which lower socio-economic groups have become unnecessarily disadvantaged (not pretending that they have not always been so). The logical location for unskilled and semi-skilled workers is still at the centre of the city, or at strategic points on the public transport system. Even with the flight of much industry to the urban fringe we must remember that such labour has to be very mobile and generally will gain greater accessibility to the urban labour market, and at less real cost, by using public transport, if located near the old city core. The C.B.D. itself still provides considerable employment for this group, and lower-income groups have been displaced to the periphery by (a) urban renewal and (b) public housing policy.

Measures to deal with so-called 'slum clearance' and 'urban renewal' whether in England, the U.S. or Australia, have been largely counter-productive. Even the English new town program, largely conceived as a way of limiting the size of London, stopping the drift to the South East and dealing with the East End, has had very limited economic success and much social failure. Only now, after 25 years, are the initial new towns beginning to develop social pathologies as 'good' as the old slum cultures.

In the U.S.A. urban renewal has largely lowered the stock of cheap housing, provided new inner urban housing for the middle class and the rich, and subsidized business interests. The much publicized New Haven renewal program under Mayor Lee and Ed Logue has been characterized as a Democrat measure to subsidize Republican businessmen. Some economic analyses even suggest that much commercial renewal would have taken place anyway and would have used private sector finance.⁴

The operation of Australia's public housing has also had disadvantages for lower-income groups. (The controversy over slum clearance in Melbourne is a reflection of the U.S. conflict of 8-10 years ago.) Until very recently our housing program has been seen, and it is still operating, as a way of providing a cheap house on a cheap

² For an excellent survey of these attitudes see White, M. & L., *The Intellectual Versus the City*. New York, Mentor Books 1964. Also see Glass, R., "Anti-Urbanism" *Current Sociology* (4) 1955, pp. 5-19, repeated in Stewart, M. (ed.), *The City: Problems of Planning*, Penguin 1972.

³ For a comprehensive survey see a paper by a group of staff and students from the Department of Environmental Design, T.C.A.E. 'Optimum City Population and Optimum Living Densities—Useful Concepts?' The paper was delivered to a symposium on 'Limits to Growth: Population in Australia' at the 45th ANZAAS Congress at Perth 1973.

⁴ e.g. see Anderson, M., *The Federal Bulldozer: A Critical Analysis of Urban Renewal 1949-1962*, Cambridge, Mass. M.I.T. Press 1964.

block.⁵ In other words it has been putting a roof over poverty. The need to reduce land costs has forced housing authorities to purchase fringe broad acre land and as a result create large low-income ghettos. In the nineteenth century city there was closer grain mix of social classes.

Very largely, lower income families cannot provide their own housing because (1) they do not have enough money, (2) they do not have access to credit, (3) they have not had the experience to plan their expenditure, (4) they may have pressing personal difficulties, e.g. no husband, which exacerbate 1, 2 and 3. Measures to meet these problems should be largely financial and of a supportive social and educational nature.

And I suppose that many of the upper middle class, especially professional and academic groups, think that there is something wrong with the physical and visual environmental quality of the city. This is a very complex question. The upper middle class can afford to worry about physical appearance and town planning. The Garden City movement, and the City Beautiful movement were all heavily permeated with physical determinism, which in its crudest sense implied that beautiful cities produce beautiful people. However, one must reflect that these movements were often elitist and anti-democratic. There are tremendous links between the early conservation groups, the town planning movement, the city manager development and the scientific management thrust. All seem to distrust democratic conflict and suggest hierarchical models of government or management. I always think that it is sobering to look back through history and note that it is the conservative or tightly controlled societies that produced visually ordered and 'beautiful' cities. For many western eyes it is the designed Renaissance city with tighter central control rather than the organic and 'messier' mediaeval city, that is the ideal concept of urban beauty. We still talk of 'civic design'.

There is another area of real concern in the urban condition. This is the operation of one purpose agencies, particularly at the metropolitan level of infrastructure or basic service systems. Separate authorities for water, highways, public transport, communications, and major social facilities all develop their own programs with little effective co-ordination or concern for the impact of

their operations, other than in terms of their own measures. One can discuss the freeway problem in terms of a lack of decision-making structure to develop proposals in relation to the total infrastructure, as well as in terms of the problems of narrow engineering-based development authorities with techniques and resources in search of problems to which they can apply preconceived solutions.

The mass of separate local government units which constitute even a small urban area of 50,000 people also makes infrastructure co-ordination very difficult.

What is the 'urban crisis' then? I would suggest, with many others, that we are really witnessing the problems of a society in transition from the industrial to the post industrial culture⁶ and that many of our problems stem from the style of thought and institutions that were appropriate in the early stage of primitive industrialization. Even our party system of government with departmental administration is out of date. It is excellent for dealing with simple development problems such as build a railway, build a highway, or with quantitative social issues such as institute compulsory schooling, increase the school leaving age to 14, build a public high school. In that type of issue, competition between claims for resources can easily be resolved by a cabinet model of political trading. Not a great deal of infrastructure co-ordination is required.

We are now moving into a different social situation. The issues we face are not of the same order. We are concerned with choosing between alternative mixes of transport, inter-relationships between alternative transport systems and land use, trade-offs between building housing or providing credit for the poor, varieties of education to satisfy individual differences and develop flexibility to meet increasingly rapid change. All of these are, in government terms, inter-departmental, and the current political model (i.e. the cabinet model or the political committee) cannot carry out the complex task of co-ordination.

The representative government model is also not fitted to deal with qualitative issues at the micro-level.⁷ Whether these be physical issues such as the visual environment, or social issues

⁵ For excellent analysis of the social problems of public housing see Newton, P., 'Housing Policy and Housing Choice', unpublished Dip.Arch. Thesis, Department of Environmental Design, T.C.A.E. 1970, and Jones, M., *Housing and Poverty in Australia*, Melbourne University Press, 1972.

⁶ The work of Mel Webber and Ed Banfield in the U.S.A. is of importance here e.g. see Banfield's 'A Critical View of the Urban Crisis', *Annals of the American Academy*, Jan. 1973, pp. 7-14. For a popular presentation see Alvin Toffler's *Future Shock*, Pan 1971.

⁷ For a simple presentation of this issue see the Skeffington Report *People and Planning*, H.M.S.O. London 1969.

such as educational goals and methods, centralized decision-making and centralized standards are no longer appropriate. Indeed, given the present conflict between citizen groups and governments, they are no longer practical.

What action then does this analysis suggest? At the administrative and governmental level it supports a familiar concept quoted at the beginning of this paper: functional regional government for urban areas with sophisticated planning procedures and the elimination, or at least integration, of the one purpose agencies. However, I would submit that it also suggests a need for considerable decentralization, indeed local control, over micro-environmental questions in living areas, and over the qualitative aspects of social services, e.g. schools and health centres. And this means local control at a scale considerably less than present local government units, which are too small to deal with urban infrastructure questions and too big to deal with qualitative issues.

The achievement of this state of affairs is possible in the near future if a locus of considerable centralism, Canberra, distributes its funds in certain ways:

1. No funds should be provided to local government or special purpose agencies unless their proposals are part of a regional infrastructure plan, or have, in the short term, been reviewed by a regional agency.

2. Funds should be made available to local neighbourhood groups for such matters as rehabilitation, historic preservation, open space and playgrounds, pocket car parks, community programs, children's play groups, etc. Such funding could foster the establishment of neighbourhood development corporations as happened in a few cases with the U.S. Model Cities program.

3. Funds should be made available for planning and participation at the regional and neighbourhood level, especially for goal formulation exercises.

What then would be the impact on the role of the environmental design professions and their operation?

Most importantly, there would be a need to change philosophical orientation on the part of many of the professionals who tend to be elitist and anti-democratic. There would be a need to recognize that the total process is towards one of variety and pluralism. The objective of urban planning and architectural design should be to maximize choice and increase freedom. Too many planners, engineers and architects seem to

think they have *the* answer and that the participation process is essentially one of selling rather than learning. They must recognize that plans are only *means* to achieve goals and objectives. They also must appreciate that community goal formation in the post-industrial society is too complex and serious an issue to leave to the traditional political system.

Environmental design would be very much a two-scale operation⁸. At the regional scale one would be concerned with large scale structure questions: water supply, transport, and major land use decisions such as location of commercial facilities, major industry, major social facilities. At the local neighbourhood scale the issues would be the traditional physical design and qualitative matters that at the moment are so unfortunately intermixed with structure questions. Interdisciplinary planning of the optimizing mode is appropriate and necessary at the regional level. Systems analysis and cost benefit techniques would be used, and could be used, since funds, data, staff and time would be available. At the local level traditional group conflict and qualitative approaches would tend to apply.

The professionals at the regional level would have to deal with the major environmental impact questions ranging from the ecological capacity of the regional system to the local impact of freeway construction. The regional planning task would require a different type of environmental design professional from those we are currently producing in engineering, architecture and planning. He would have to be capable of working in interdisciplinary teams, and require a good general education, a high level of specialist skill and a problem orientation. Australian tertiary education is still producing professionals in separate departments, with little or no general education or appreciation of the urban system, and with a set of techniques or solutions rather than a problem-solving orientation.

At the local level one can already see a new professional role developing: the concept of the planner or the architect as an advocate, either for groups within the local area, or for the local area to the regional system. This postulates a new democratic orientation for the designer and a wider social and political/legal capacity than previously. It also suggests that this role of the professions will become more 'public', in the sense of urban extension services or community or store-front environmental design offices.

⁸ The reform of British planning legislation which was carried out in the 1960s and culminated in the 1968 Act is largely based on these principles.

I have talked then of the urban situation, possible courses of reform and the likely impact on the roles of the environmental design professions. Is there a general direction in this analysis?

I would suggest that not only is there a development towards greater pluralism in a social sense but there is also a development towards democratic environmental design, i.e. greater freedom for individuals to determine their own environment. A regional/neighbourhood structure allows

for this and at the same time provides a more effective feed-back or learning system. It allows greater numbers to learn to design their own environments and therefore come to design their future by learning also to control their own community planning processes and social institutions, and contributing to the regional decision-making process. This is necessary if we are not to continue our present habit of rushing backwards into the future.

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1973

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ABRIDGED REPORT OF COUNCIL

FOR THE YEAR ENDING MARCH 8, 1973

MEETINGS AND LECTURES

- MARCH 9—*Biological Aspects of Zero Population Growth*. Professor P. Angas Parsons.
- APRIL 13—Joint Meeting with the Institute of International Affairs (Victorian Division). *Legal Control of the Australian Seabed*. Professor D. P. O'Connell.
- MAY 11—*Education, 1972 to 2002*. Professor R. J. Goldman.
- JUNE 8—Medal Lectures: *X-ray Diffraction and Chemical Bonding*. Dr. B. Dawson.
The Future of Pesticide Research. Mr. A. Baklien.
- JULY 13—Symposium: *A Scientific Basis for Urban Planning*. Mr. K. Grant, Dr. J. Brothie, Mr. R. Arnot and Mr. K. Tyler.
- AUGUST 10—*New Findings in Medical Science*. Professor R. D. Wright.
- SEPTEMBER 14—Symposium: *Bass Strait, its Coasts and Islands*.
- OCTOBER 12—*The Murchison Meteorite and Evolutionary Theory*. Dr. R. B. Johns.
- NOVEMBER 9—Soiree: *Recent Work by ANARE on the Amery Ice Shelf and the Lambert Glacier*. Mr. I. Allison.
- DECEMBER 14—*Fungi associated with Root-rot of Subterranean Clover*. Professor L. L. Stubbs.
Phytophthora cinnamomi, the cinnamon fungus, a threat to our forests and national parks. Dr. G. Weste.

Attendances at Ordinary Meetings of the Society totalled 785.

MEMBERSHIP

Mr. E. D. Gill was elected a Life Member *honoris causa*. Membership at 28th February 1973 was: Honorary Life Members 3, Life Members 31, Members 505, Associates 77. Total, 616.

Council recorded with regret the deaths of Mr. R. A. Dunn, Dr. D. Lafeber, Dr. F. L. Miller, Mr. T. E. Neville Payne, Sir Samuel Wadham, Mr. L. R. Whitby and Mr. N. A. Wakefield.

SAMUEL MACMAHON WADHAM came from Cambridge to the Chair of Agriculture in Melbourne in 1926 and soon came to terms with the variety and difficulties of Australian agriculture. He was a member of the Royal Commission on the Wheat, Flour and Bread Industries in the 30s and of the Rural Reconstruction Commission in the 40s, and co-author with Professor G. L. Wood of the book *Land Utilization in Australia*. He was knighted in 1956 and retired from the Chair in 1957 with the honour of Emeritus Professor. He became a member of the Society in 1927, was a Councillor from 1933 to 1961 and President in 1937-1938, a Trustee from 1953, and was elected a Life Member *honoris causa* in 1971. He died in September 1972 in his 81st year.

NORMAN ARTHUR WAKEFIELD spent his boyhood and the early years of his teaching career in the

remote Eastern parts of Victoria, where there were good opportunities for botanical exploration. He published 126 articles in the *Victorian Naturalist* including descriptions of 39 new species of vascular plants, and six papers in the Society's *Proceedings*. He was elected an Honorary Life Member of the Field Naturalists' Club in 1956, and was awarded the Australian Natural History Medallion in 1962. He became a member of the Society in 1961. From 1965 he lectured in biology, first at the Melbourne, then at the Monash Teachers' College. He had a part in the recent discovery of amphibian footprints in Devonian sandstone on the Genoa River. He died suddenly, from a tragic accident, in September 1972.

PROCEEDINGS

During the year the Society published Volume 85, Part 1, of *Proceedings* at a cost of \$2755. Council acknowledges with gratitude grants towards the cost of publication from the Government of Victoria and the Universities of Melbourne and New England.

LIBRARY

2614 volumes and parts were received during the year, mainly from exchanges with 62 Australian and 274 overseas organizations. 475 items were borrowed. A request was received from the Emperor of Japan for a copy of Vol. XXIII (O.S.) of *Proceedings*. A bound copy was given to the Emperor, who graciously presented to the Society copies of 3 papers on marine biology written by him.

HALL

In addition to the Society and the Royal College of Obstetricians and Gynaecologists, 16 professional and other bodies held 75 meetings on the premises.

A ventilating fan has been installed in the Lecture Hall.

FINANCE

The Society remains in a sound position. Withdrawal of Book Bounty has adversely affected the cost of publishing *Proceedings*. Increased expenditure on maintenance of the Hall and cottage will be required in the next few years.

ACKNOWLEDGMENTS

Council expresses its thanks to the many persons and organizations who have given valuable assistance during the year: Mr. H. G. Stevens, Honorary Auditor; Mr. F. Suendermann and Mr. N. Straehan on behalf of Sir Roy Grounds (Honorary Architect); ICI Australia Ltd; The Parks, Gardens and Recreation Department of the Melbourne City Council and Mr. and Mrs. A. Sadik.

A. DUNBAVIN BUTCHER,
President.

INDEX TO VOLUME 86

A		M	
Abele, C.	143	McEvey, A. R.	151
Ages of Tertiary Basalts, Victoria	143	McNeill, Barry	227
Aireys Inlet, Ages of Tertiary Basalts at	143	Macquarie Island	
Australian Cainozoic Brachiopods	111-131	Fossil Penguin Bones from	151
		Opisthobranch Molluscs from	39
		Maude, Ages of Tertiary Basalts at	143
		Marine Shells, Geochronology of	35
		Molluscs, Opisthobranch	39
		Mountain Ducks	1
B		N	
Beavis, F. C.	175	Nelson, P. E.	19
Beavis, Sara	175	Norman, F. I.	1
Black Ducks	1	<i>Nothofagus cunninghamii</i>	
Brachiopods, Australian Cainozoic	111-131	Ecotonal Stages	137
Burgess, L. W.	19	Rainforest, Distribution of	47
Burn, Robert	39		
C		O	
Cainozoic Brachiopods, Australian	111-131	Obituary Notices	234
Clover, Subterranean, Root Rot of	19	Ogle, H. J.	19
Computer Simulation Study	85	Opisthobranch Molluscs	39
Conodonts	77		
Cooper, B. J.	77		
Croydon Sunkland, Victoria	15		
D		P	
Devonian, Lower	77	Page, R. W.	143
Ducks, Movement and Mortality Patterns	1	Parsons, R. F.	29
		Penguin Bones, Fossil, from Macquarie Island	151
E		R	
Ecology, Methods in	85	Radiocarbon Dates, Victoria. Second List.	133
Edgerton, J. P.	19	Richardson, Joyce R.	111-131
Ettershank, Daphne L.	85	Root Rot, of Subterranean Clover	19
Ettershank, G.	85	Royal Society of Victoria	
<i>Eucalyptus</i> Species, Disjunctions in Distribution	29	Abridged Report of Council	234
		Officers	233
F		S	
Fossil Penguin Bones	151	Sale, E. Victoria, Marine Shells from	35
Fungi, Biology of	19	Schornick, James C., Jr.	35
		Stubbs, L. L.	19
		Subterranean Clover	19
		Symposium, 'Urban Environment and Life'	215
G		U	
Garratt, Michael J.	15	Urban Environment and Life, Symposium on	215
Geochronology of Marine Shells	35		
Gill, E. D.	133, 151		
Graptoloids, Victoria	175		
H		V	
Heard Island, Opisthobranch Molluscs from	39	Vestjens, W. J. M.	151
Howard, Truda M.	47, 137	Victoria, Radiocarbon Dates	133
		Victorian Isograptids	175
I		W	
Isograptids, Victorian	175	Wadham, Sir Samuel MacMahon. Obituary	
		Notice for	234
K		Wakefield, Norman Arthur. Obituary	
Kaufmann, George A.	223	Notice for	234
L		Y	
Loyola, Victoria, Conodonts from	77	Yencken, D. G. D.	215

9/2

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P. 100000